

VEGETATIVE REGENERATION IN WETLAND  
FORESTS OF FLORIDA

by

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Abstract of Dissertation Presented to the Graduate School  
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VEGETATIVE REGENERATION IN WETLAND  
FORESTS OF FLORIDA

by

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Major Department: Botany

Environmental stress on plants limits reproductive success, often with differential effects on vegetative and sexual reproduction. Effects of stress on reproduction differ among species depending on degree of stress tolerance and capacity to recover following stressful events. Consequently, relative contributions of seedlings and sprouts in natural communities vary with disturbance regime and community composition.

This study investigated the relationship between hydrologic regime and basal sprouting of trees in north-central Florida wetlands. Basal sprouting patterns in natural wetlands were compared with sprouting responses in those parts of the Oklawaha River floodplain that had been artificially impounded for 18 years. Interpretations of

sprouting responses in relation to hydrologic regimes were based on experimental investigations of apical dominance mechanisms.

Trees sprouted throughout the range of natural hydrologic settings. The relative abundance of sprouts in natural communities depended on tree species composition and growing conditions. Sprouts were generally more common among dicots rooted on hummocks in wetlands with brief but frequent periods of deep inundation.

Stems that originated as basal sprouts were common in natural, unimpounded portions of the Oklawaha River floodplain forest but became more abundant with increasing water depth in Lake Oklawaha. Trees have persisted in the reservoir either by simply tolerating altered hydrologic regimes or by increasing sprout production, thereby rejuvenating individuals. Contrary to predictions from earlier studies of this system, species richness has remained high in standing water depths up to 0.6 m due to this sprouting response.

Experimental investigations of apical dominance mechanisms showed that inundation does not affect sprout production either by direct anoxia-induced physiological responses or indirect responses to altered root-to-shoot ratios following inundation. Flooding inhibited growth of sprouts, as well as of parent stems, due to increased stomatal resistances.



Successful regeneration by wetland trees depends on avoidance of inundation; continual production of basal sprouts and rapid sprout growth are primary factors contributing to the success of vegetative regeneration in wetlands. Successful vegetative regeneration after disturbances such as inundation reduces species turnover rates, stabilizes community structure, and provides a survival mechanism that allows individuals to survive despite long-term stress.

CHAPTER 1  
PATTERNS, PROCESSES AND MECHANISMS OF  
VEGETATIVE REGENERATION

Introduction

Regeneration of wetland plants is limited by the presence of excess water. Seeds of most species do not germinate under water, and seedlings die if submerged. Establishment is, therefore, restricted to extended periods of soil exposure during which seedlings can grow above the deleterious affects of subsequent inundation. Annual inundation of natural wetlands is, however, fairly predictable (sensu Colwell 1974), and suitable periods for seedling establishment in wetlands are infrequent. Alternatively, angiosperms and certain gymnosperms are capable of sprouting, a form of vegetative regeneration, which may not depend upon exposed soils.

Population regeneration and survival depend on interactions between genetically controlled characteristics, such as sprouting, and the environment (Bazzaz 1984). In wetlands, where seedling establishment is relatively uncertain (Huenneke and Sharitz 1986), relatively greater investment by populations in vegetative regeneration may be advantageous.

Patterns, processes, and mechanisms of vegetative regeneration are therefore integral to the understanding of plant demography and ecology in wetlands and in other natural systems in general. In order to understand patterns of vegetative regeneration and the role of sprouts in wetland community dynamics, it is necessary to determine what species-specific and environmental conditions affect sprout initiation, growth, and survival.

#### Definition of Vegetative Regeneration

Vegetative regeneration is the production of genetically identical offspring that often remain physically and physiologically connected to the parent stem (Silvertown 1984, Pitelka and Ashmun 1985). Through vegetative regeneration, genetic individuals are able to increase stem numbers, disperse into under-exploited areas (e.g., Holbrook and Putz 1982), expand areas of dominance (e.g., gap closure), recover from injury (Powell and Tryon 1979, Malanson and Westman 1985, Terwilliger and Ewel 1986), and survive in spite of severe or chronic stress (Held 1983, Paillet 1984).

Plants use a variety of mechanisms to reproduce vegetatively. Regeneration and dispersal of ramets (genetically identical individuals) are often accomplished with rhizomes and stolons. Vegetative reproduction of individuals capable of independence from the parent stem is also possible by

division of underground bulbs, tillering, and air-layering. Vegetative expansion, recovery, and maintenance of individual stems, however, are the results of sprouting: the production and expansion of buds.

Sprouts arise from either axillary or adventitious buds (Esau 1960). Axillary buds differentiate from leaf tissue as meristematic cells in axils of leaf primordia. When axillary buds remain dormant, secondary growth carries the bud away from its point of origin; vascular connections with the main axis are developed and maintained. In contrast, adventitious buds develop from meristematic cells differentiated from callus tissue and may arise during any point of development, either on the stem surface or deeply seated in stem or root tissues.

Sprout type can be determined by the bud origin, location on the stem, and conditions that stimulated bud growth (Kramer and Kozlowski 1960). For example, basal or stump sprouts often arise from dormant buds on the lower tree trunk or root crown. Epicormic branching, dormant buds sprouting on main stems and branches, is often associated with increased light levels (Blum 1963, Smith 1966, Trimble and Smith 1970, but see Wilson 1979, Bryan and Lanner 1981). Root sprouts are adventitious.

### Consequences of Vegetative Regeneration

The degree to which plants are able to produce sprouts and the effect of sprouts on plant survival have important implications for population and community dynamics. The principal effect of sprouting is the reduction of mortality rates of established genetic individuals. Increased plant longevity stabilizes populations, while genetic variability is maintained (Hamrick 1979). Species turnover rates are slower and possibly arrested in communities with a high proportion of species that can sprout. This is apparently the case in some mature plant communities that are stable in species composition (Odum 1969) and have relatively more successful vegetative than sexual reproductive efforts (Abrahamson 1980).

Interpretation of stand age structure and history becomes more complicated when age distributions of stems do not match root age distributions. For example, 58% of seedlings sampled in hardwood forests of central Pennsylvania had younger shoots than roots; young stems had roots ranging up to 25 years old (Ward 1966). Under these conditions, standard population ecological methods using stem size distributions to deduce age relationships and patterns of regeneration and mortality of genetic individuals are

inadequate. Application of models describing density-dependent relationships and competition for resources becomes very difficult in communities with a high rate of sprouting.

Sprouting has further consequences for natural selection and population distributions. For example, competition among genetic individuals over time results in locally adapted clones (Abrahamson 1980). Furthermore, spatial distributions of ramets are generally more aggregated than are genetic individuals (Huenneke 1985).

### Phenotypic Plasticity

Phenotypic plasticity is variation in expression of a character that can be altered by environmental conditions (Bradshaw 1965). Degree of plasticity is variable both within and among species. Consequently, the degree of character plasticity is species-specific, varies with environmental conditions, and is alterable by selection (Abbott 1976a).

Environmental conditions influence plant phenotypes by inducing changes in physiological and morphological characters and by favoring existing phenotypes, particularly if environmental changes are rapid (Bradshaw 1965). Phenotypic plasticity has been noted in response to many environmental conditions, including inundation, degree of exposure, and fertilization. For example, finely dissected leaves are

found on submerged portions of aquatic plants, such as Utricularia inflata Walt. and Myriophyllum heterophyllum Michx., while emergent leaves of the same plant are entire (Godfrey and Wooten 1981). Genetic variability often parallels variation in exposure; the relative dwarf habit of Senecio vulgaris L. progeny from plants exposed to strong winds on a cliff site in Wales was retained throughout development, but there was greater variation in heights of progeny from sites with variable levels of exposure (Abbott 1976b).

Phenotypes tolerant of rapid environmental changes are favored when plants are unable to avoid damage (Bradshaw 1965). For example, Held (1983) reported a partial shift from seedling establishment of American beech (Fagus grandifolia Ehrh.) toward regeneration by root sprouts in areas where the climate is severe, presumably because root sprouts are more tolerant of freezing than young seedlings. Similar trends were reported from tropical deciduous and subtropical forests of India (Khan et al. 1986).

Increased longevity of sprouting individuals increases the chances that plants will experience changes in environmental conditions. Long-lived perennial plants exhibit a large degree of phenotypic plasticity by sprouting under different environmental conditions (Jefferies 1984). For example, allometric diversity of sprouting plants allows adjustment to changes in availability of water, major

inorganic nutrients, light, and carbon dioxide, and to shoot and root pruning (Wilson 1988).

### Distribution of Vegetative Regeneration

Patterns of sprout production are the result of interactions between a species' propensity to sprout (i.e., species-specific apical dominance strength) and environmental conditions. Under environmental conditions favorable for sprout production, species will differ in sprout production rates depending on their specific strengths of apical dominance (Kramer and Kozlowski 1979). Within communities, proportions of stems of sprout origin are therefore partially a function of species composition.

Sprout production is more common in lower plants and angiosperms than gymnosperms due to the typically strong apical dominance exhibited by the latter (Kramer and Kozlowski 1979). Abrahamson (1980) reports variable occurrences of vegetative reproduction in angiosperm-dominated communities. Plants commonly reproducing vegetatively have been reported from all latitudes and for both terrestrial and aquatic species. The relative importance of vegetative to sexual reproduction of trees, however, decreases in the tropics.

Sprouting is thought to be favored in late successional and disturbance-maintained communities (Bradshaw 1965, Abrahamson 1980), as well as under severe environmental



conditions (Held 1983, Khan et al. 1986). Tree seedlings of northeastern deciduous forests survive long periods of suppression in unfavorable understory conditions partially by replacing dead stem apices with sprouts (Powell and Tryon 1979). Above-ground portions of shrubs and trees can recover following fire damage by the production of stump sprouts and epicormic branching (e.g., Ewel and Mitsch 1978, Ohmann and Grigal 1981, Malanson and Westman 1985). Finally, American chestnut maintains individuals following devastation by the chestnut blight by the persistent production of sprouts (Paillet 1984).

#### Sprouting in Stressful Environments

Sprouting frequency is often high in plant communities subjected to natural stress-inducing disturbances of various intensities, frequencies, and forms (Bazzaz 1983). Physiological stress is imposed on plants subjected to wind (Putz and Brokaw 1989), extreme temperatures (Held 1983), grazing, fungal or insect infestations (Paillet 1984, Maschinski and Whitham 1989), logging (Terwilliger and Ewel 1986), unstable soils (Mooney and Billings 1961), increased exposure from community fragmentation (Trimble and Smith 1970), drought, and excess water (Johnson 1987). These environmental conditions can cause irreversible alterations in physiological processes (Johnson 1987); in such cases, sprout production can be considered a recovery mechanism.

Many references to vegetative responses to disturbances pertain to fire-maintained communities. For example, Keeley (1981) described the relative importance of sprout production versus seedling establishment for chaparral shrub populations. Sprout production is favored by frequent fires but seedling establishment becomes more important under fire regimes with longer fire return intervals.

Over 90% of the groundcover species in longleaf pine-wiregrass savannas of the southeastern coastal plain are capable of vegetative regeneration (Davis unpublished data). These communities are maintained by frequent low-intensity fires. Stem production and mortality rates of fire-tolerant species are determined primarily by fire frequency; seedling establishment is rare. Consequently, spatial patterns of fires carried through the groundcover determine the extent of even-aged patches of mixed-species stems.

Occurrences of sprout regeneration in wetlands have not been well documented, although note has been made that species capable of regenerating vegetatively are favored in continuously flooded sites (Malecki et al. 1983). Stress imposed on plants by long periods of inundation should affect vegetative regeneration.

#### Stress Induced by Inundation

Inundation is stressful to many plants because of its effects on aerobic biochemical processes (Ponnamperuma

1972). Oxygen diffuses through air 10,000 times faster than through water; as water displaces air from soil pores, molecular oxygen availability for respiration is greatly reduced. If aerobic organisms and organic matter are present, molecular oxygen is consumed within hours of inundation; the changing oxidation state consequently alters respiration pathways and mineral balance.

Excess water becomes physiologically stressful to plants for three reasons: anoxic conditions develop, toxins accumulate, and nutrient availability is altered (Kozlowski 1984b). Many flood-tolerant species are able to tolerate only short-term anoxia because energy production is limited by anaerobic respiration. Plant tolerance to inundation often depends on an ability to adapt metabolically and to aerate the rhizosphere (Hook 1984).

As diffusion rate of oxygen in water is slow, diffusion of toxic metabolic products, such as carbon dioxide and ethylene, is also limited. In addition, increased concentrations of iron and manganese with reduced oxidation state result in phytotoxic concentrations. Again, the capacity of the plant to aerate the root system, thus oxidizing many toxins, is an important flood-tolerance mechanism (Hook 1984).

Stomatal closure is often the initial response to root system inundation; consequently, transpiration and photosynthesis rates are reduced (Kozlowski 1984a). If inundation

continues additional stress symptoms, such as leaf epinasty, chlorosis, and root mortality, develop in relatively flood-intolerant species; ultimately, flood-intolerant species die (Gill 1970).

Flood-tolerant species, particularly woody angiosperms, develop physiological, morphological, and anatomical adaptations to increasing levels of stress due to anoxic soils (Gill 1970, Hook 1984). Short-term flooding induces reversible alterations of metabolic processes, such as glycolysis and growth rates, whereas long-term flooding is more likely to induce irreversible morphological and anatomical changes.

Anatomical and morphological adaptations of flooded plants primarily increase aeration of flooded roots. Development of aerenchyma, lenticel formation and hypertrophy, and pneumatophore production form an aeration system throughout the flooded portion of the plant. Although roots are often lost following inundation, flood-tolerant species regenerate new roots on the original root system, on the submerged part of the stem, or on both (Kozlowski 1984c).

Intensity of anoxia-induced stress is related to duration, depth, and frequency of inundation. Root mortality rates of artificially impounded floodplain trees increase with depth of inundation due to corresponding increases in anoxia of the inundated soils (Harms et al. 1980). Due to a mixing effect that carries oxygen throughout the water

column, however, flowing water is less detrimental to plants than standing water (Kozlowski 1984c).

Depth, duration, and frequency of inundation differ among wetlands. Variations in water sources (i.e., runoff, groundwater, and throughfall) and water loss (i.e., outflow, evapotranspiration, and percolation) determine the site-specific hydrologic regime (LaBaugh 1986), and consequently the intensity of anoxia-induced stress. For example, cypress domes (hydrologically isolated wetlands common in the southeastern coastal plain) receive little runoff from surrounding drainage basins and do not drain to communities at lower elevations; their hydrologic regimes are characterized by slow seasonal fluctuations (Heimburg 1984). Rivers, in contrast, receive a large proportion of water by runoff from upstream sources in addition to base water flow, which flows rapidly through and out of the system; as a consequence, floodplain forests are typically inundated frequently for relatively short durations (Wharton et al. 1982). Greater degrees of anoxia are expected in cypress dome substrates than in floodplains.

#### Mechanisms of Apical Dominance

Initiation of growth of lateral buds follows release from apical dominance (Rubinstein and Nagao 1976, McIntyre 1987, see Zimmerman and Brown 1980). Removal of apical buds or girdling stems below apical buds often results in lateral

bud growth. The most commonly noted condition that stimulates sprout production is direct injury or removal of some portion of the plant. Coppice growth occurs in response to cutting (Hook et al. 1970, McGee 1975), mechanical damage (e.g., Putz et al. 1983, Gartner 1990), and fire (Malanson and Westman 1985), as well as insect and fungal infestation (Paillet 1984, van der Meijden et al. 1988). Root sprout production is thought to be stimulated by abrasion or freezing and thawing (Jones and Raynal 1987).

The mechanism of release from apical dominance is often ascribed to removal of the source of auxin, a class of plant growth-promoting hormones, and a reduction in the auxin-to-cytokinin concentration ratio at the lateral bud; the initiation of lateral bud growth can be stopped by external applications of auxin (Rubinstein and Nagao 1976, Powell 1987). This mechanism explains the phenomenon of sprout production under a variety of environmental conditions such as fire or insect infestation, but not necessarily in plants stressed by inundation. Whereas mechanically injured trees in wetlands produce sprouts, there is no visual evidence, such as canopy stress or suppression, to explain the initiation of sprout growth by the majority of trees with normal water level fluctuations. Furthermore, stem concentrations of auxins may increase following inundation while cytokinin production is reduced (Reid and Bradford 1984), conditions increasing the auxin-to-cytokinin ratio that reinforce

rather than reduce apical dominance (Salisbury and Ross 1985).

McIntyre (1987) suggested an alternative hypothesis to explain the mechanism of apical dominance: growth of lateral buds is initiated when sink strength of lateral buds for stem water increases relative to apical bud strength. Lateral buds of pea and sunflower seedlings were induced to grow under high light and high nutrient conditions when the relative humidity was increased to near 100%. Sink strength of the apical stem for stem water was reduced relative to the sink strength of the lateral buds as transpiration rates of the seedlings were reduced, but xylem water potentials remained high. This mechanism does not depend upon plant hormone concentrations for initiation of lateral bud growth. (Auxin concentrations, however, are presumably important for continued growth of the sprout through their effect on cell differentiation and strengthening of the vascular connection between the developing sprout and parent stem.)

Wetland tree species differ in their tolerance to inundation (Hosner 1960, Gill 1970). Survival following inundation depends upon how quickly the tree can resume normal function. Stomatal closure, a common initial response to flooding, interrupts normal rates of both photosynthesis and transpiration (Kozlowski 1984a). For example, cherrybark oak (Quercus falcata var. pagodaefolia Ell.) is flood-intolerant as evidenced by closed stomates for weeks

following inundation (Pezeshki and Chambers 1985b). Pereira and Kozlowski (1977) showed, however, that stem water potentials of inundated wetland trees remain high during periods of stomatal closure.

Reduced transpiration demand by apical portions of stems and available stem water below the apex are suitable conditions for release of lateral buds from apical dominance. Under these conditions, duration of the period of stomatal closure following inundation should be related to the propensity of that species to produce sprouts in natural wetlands. Lateral buds of those species with rapidly opening stomata following inundation are least likely to have time for lateral bud release (i.e., initiation of sprout growth) before normal transpiration rates resume. Conversely, species with slowly opening stomata may have adequate time for lateral buds to initiate growth and increase their sink strength for stem water before the parent stem resumes normal functions.

### Research Objectives

Reproduction is limited in disturbance-maintained plant communities by periodic stressful or destructive events, such as fire, grazing, or drought. Seedlings are particularly susceptible to stress and damage, especially during early establishment phases when energy reserves are inadequate for recovery. Sprouting is common in these



communities; sprouts are formed rapidly by parent plants and benefit from parent resources for rapid growth.

Relative proportions of stems established as sprouts or seedlings have been related to disturbance regimes (Keeley 1981). Frequent low-intensity disturbance events often favor sprout production; seedlings are unable to become established, yet recovery time for sprouting individuals is sufficient to replenish energy reserves before a subsequent stressful event.

Inundation of wetland communities is a periodically occurring stressful phenomenon analogous to other disturbance regimes. Whereas, for example, fire regimes are described in terms of intensity and frequency, degrees of anoxia-induced stress depend on duration, depth, and frequency of inundation. Effects of fire on sprouting individuals are clearly definable as the removal of stems followed by a pulse of high nutrient availability; interactions of inundation and mechanisms of sprout production, however, are not so clear.

The research addressed in this report falls into three phases. The first two are descriptions of sprout distributions in the chronically stressed wetland forest of Lake Oklawaha (Chapter 2) and in natural forested wetlands with different hydrologic regimes (Chapter 3). Sprout production patterns in these wetlands were related to several environmental parameters estimating degree of anoxia-induced

stress. Interpretation of environmental correlates with sprout production, however, required a third research phase: experimental investigations of interactions of environmental conditions with mechanisms of apical dominance (Chapter 4).

Sprout production by floodplain tree species apparently increased following the creation of Lake Oklawaha in 1968 by artificially impounding a portion of the Oklawaha River. Parts of the floodplain forest have been inundated continuously for over 18 years; depth of inundation varies with location in the lake. Stress levels experienced by this forest exceed levels prior to impoundment due to the duration and, in most areas, depth of inundation. Analyses were made of sprouting production and proportions of stems of sprout origin with increasing depth of water.

Twelve natural wetlands were selected to represent the range of hydrologic conditions in swamps of north-central Florida. Several tree species commonly occur in three or more of these wetlands; these populations experience different hydrologic regimes. Sprout patterns resulting from species-specific characteristics and site-specific environmental conditions were identified at both species and community levels.

Comparisons of sprout distributions in Lake Oklawaha with those in natural wetlands isolated effects of site-specific selection pressures and stress-tolerance threshold levels. Wetland populations undergo site-specific selection

for flood tolerance, as well as other characteristics. Consequently, patterns of sprout production in natural wetlands may not be directly related to flood tolerance but only correlated with those characteristics that increase the flood tolerance of an individual. Trees of the Oklawaha River floodplain forest developed under the same hydrologic conditions; correlations of sprouting with altered hydrologic conditions are therefore independent of site-specific selection pressures and serve as controls for correlations found elsewhere.

Relationships between sprouts and hydrologic parameters are not expected to be linear across all stress levels; for example, there is likely to be a stress threshold beyond which neither sexual nor vegetative reproduction is successful. Trees in Lake Oklawaha were flooded to depths greater than are found where trees grow in natural wetlands. Upper tolerance limits of vegetative reproduction to anoxia-induced stress are clearer in Lake Oklawaha than in natural wetlands.

Correlations of sprout distributions with environmental conditions indicate processes by which the environment interacts with mechanisms of sprout production; correlations, however, can only suggest mechanisms by which a process leads to a pattern. For example, increased percentages of stems of sprout origin with inundation depth may be due to lower rates of seedling establishment in deep

water, a stimulating effect on sprout production, or both. The final experimental phase is designed to elucidate interactions of inundation with mechanisms of apical dominance and sprout initiation.

CHAPTER 2  
RECOVERY BY SPROUT PRODUCTION OF THE IMPOUNDED  
FLOODPLAIN FOREST IN LAKE OKLAWAHA, FLORIDA

Introduction

Impoundment of natural waterways creates chronic levels of stress (sensu Levitt 1972) in floodplain ecosystems. Reservoirs reduce natural water level fluctuations while increasing the depth and area of flooding in floodplain forests. The fate of the flooded forest depends on the perseverance of flood tolerant individuals (see Gill 1970). Bald cypress (Taxodium distichum (L.) Rich.), swamp tupelo (Nyssa sylvatica var. biflora (Walt.) Sarg.) and water tupelo (Nyssa aquatica L.) are examples of species generally able to tolerate continuous inundation following impoundment (Eggler and Moore 1961, Harms 1973). Many other species, which may be dominants in pre-impoundment forests, often die within a few years, changing the species composition and physiognomy of the forest (Conner et al. 1981).

Furthermore, standing water limits regeneration of many species; seedling establishment is usually precluded by constant deep flooding (Green 1947, Eggler and Moore 1961). In areas where the forest floor is rarely or never exposed

above water, sprouting is the only means of regeneration for trees (Eggler and Moore 1961, Malecki et al. 1983).

In 1968, the U.S. Army Corps of Engineers dammed a portion of the Oklawaha River in central Florida. A Federal Interagency Task Force assessed the environmental impacts of the impoundment in 1972 and 1975, 3 and 6 yr following impoundment (Gardner et al. 1972, U.S.D.A. Forest Service 1972, and Harms et al. 1980). I participated in the forest census that was repeated in 1987, 18 growing seasons following impoundment of the Oklawaha River. Objectives of the study were to describe the status of the forest after 18 years of inundation, to compare the forest structure with predictions from the earlier studies, and to characterize the strategies or patterns by which tree populations have persisted under continuously stressful conditions.

#### Site Description

The Oklawaha River (29° 30' N, 81° 50' W) flows north along the western border of the Ocala National Forest in central Florida before emptying into the St. Johns River (Figure 2.1). The climate is characterized by long, warm growing seasons (about 300 d, mean annual temperature of 21.4°C and fewer than 10 d/yr at or below freezing; Lugo and Brown 1984). Total annual rainfall is about 1300 mm (National Oceanographic and Atmospheric Administration 1986), typically with wet summers and winters. The lowest water

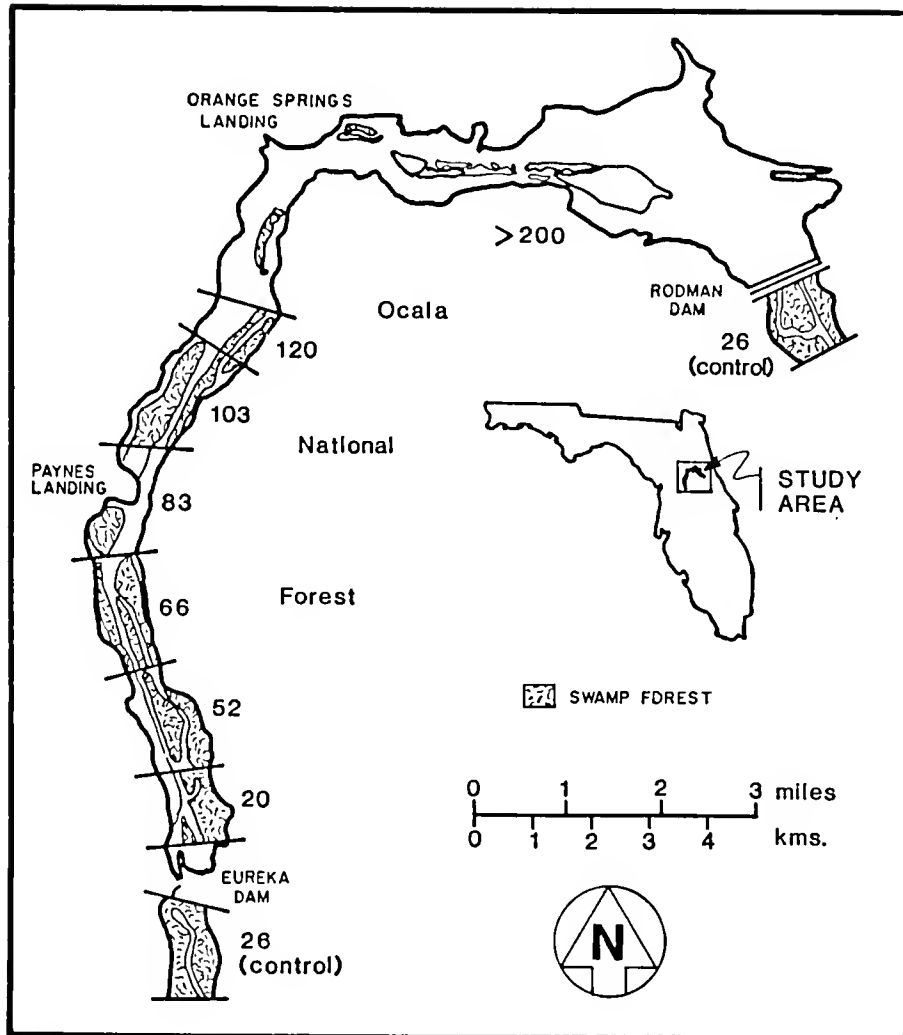


Figure 2.1. Detail of the Lake Oklawaha, Florida, study site. Lines across floodplain delineate sample populations. Numbers for each sample population indicate average water depth (cm). Note: direction of river flow is to the north (redrawn from Harms et al. 1980).

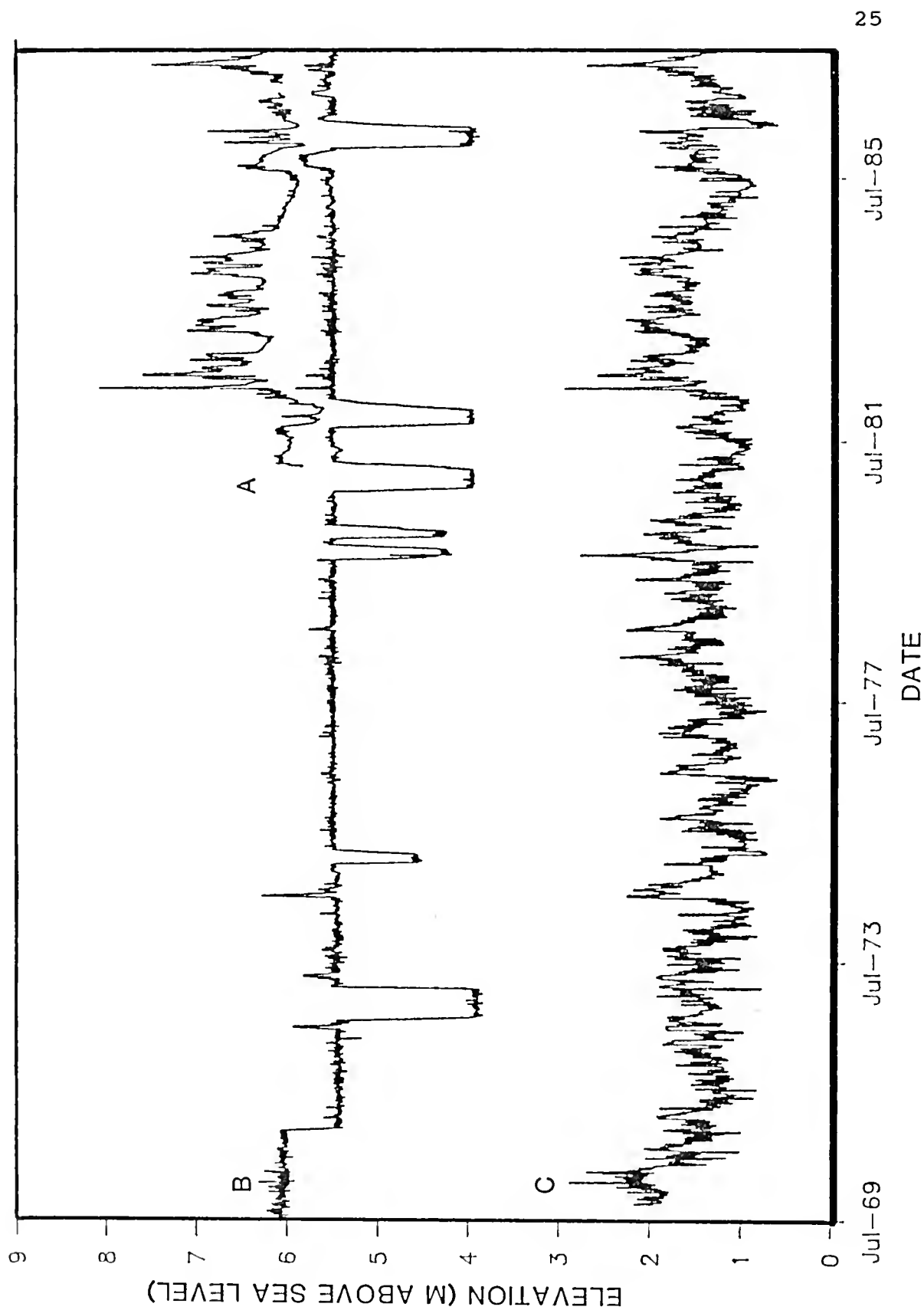
levels of the river are in May; peak water levels in September often inundate floodplain forests (Lugo 1972).

Two dams, the Eureka Dam and the Rodman Dam, were constructed on the Oklawaha River (Figure 2.1). The Eureka Dam is approximately 26 km upstream from the Rodman Dam and has never been closed; water flows north around it in the natural channel. Floodplain forests immediately adjacent to and on the upstream side of the Rodman Dam were removed before the dam was closed in 1968. The impoundment resulted in a 5265-ha reservoir, flooding most of the remaining 1620 ha of floodplain forest between the two dams.

Depths of inundation depend primarily on lake levels maintained at Rodman Dam and decrease with distance upstream (Figure 2.1). Lake level was initially held near 6.2 m above sea level for 1 year (Figure 2.2). This level corresponds to 2 m above average water level near the remaining floodplain forest in the deepest water near Orange Springs (Figure 2.1). At this time, all of the floodplain forests downstream from Eureka Dam were flooded. Subsequently, the lake level was lowered to 5.5 m above sea level, where it has been maintained except for occasional short-term draw-downs (Figure 2.2). Water depth averages 0.2 m in portions of the forest farthest from the Rodman Dam below the Eureka Dam. This is essentially natural river level. Depth of standing water in impounded forests increases to 1.2 m in



Figure 2.2. Water level fluctuations at USGS continuous recording stations upstream of Eureka Dam (A), on Lake Oklawaha (B), and downstream of Rodman Dam (C) for the period of record (A) or since the closing of Rodman Dam (B and C).



the most deeply flooded portion of the study area (Figure 2.1, Harms et al. 1980).

### Methods

The Federal Interagency Task Force censused the floodplain forest in the spring and fall of both 1972 and 1975 (Harms et al. 1980). In May and June, 1987, the forest was recensused using the stratified random sampling design of the previous censuses. Seven contiguous populations differing in average water depth were delineated along the length of the impoundment (Figure 2.1). All the populations were censused except the open water reservoir adjacent to Rodman Dam, where no live trees remained. Two control populations were delineated in the natural floodplain forest, one upstream from Eureka Dam and one downstream from Rodman Dam.

Populations were sampled with randomly located 0.04 ha circular plots, the locations of which were noted on aerial photographs (Gardner et al. 1972). Ten plots were sampled per population (except 8 plots at 83 cm; 18 plots at 103 cm; 4 at 120 cm; see Figure 2.1) for a total of 80 plots. Stems > 2 cm diameter at breast height (DBH) were measured for DBH, identified to species, and classified as live or dead.

In 1987, the previous locations of plots were approximated from the annotated aerial photographs. In addition to the above mentioned data, we noted the origin of each stem (seedling or sprout) and if the stem was producing

sprouts. A sprout was defined as the result of active growth from a bud below breast height. A parent stem can release more than one sprout; several sprouts on the same individual often survive and grow to large diameters. Stems were considered to be sprouts if they were attached at their bases with no evidence of stems of the same tree having grown together (e.g., discontinuities or seams in the bark).

Densities of live trees for the different census dates are contrasted in a repeated measures multivariate analysis of variance (GLM: SAS 1985). The lack of replication in the research design does not meet the basic assumptions of the statistical analysis; therefore, significance levels are presented only as indications of differences in tree densities between years for Lake Oklawaha.

## Results

### Species Distributions of the Natural Floodplain Forest

The Oklawaha floodplain forests, under natural conditions, are dominated by red maple (Acer rubrum L.), bald cypress, swamp tupelo, and two ash species (Fraxinus caroliniana Mill. and F. profunda (Bush) Bush; Table 2.1), which form a closed canopy 20-30 m high. Dahoon holly (Ilex cassine L.) and stiffcornel dogwood (Cornus foemina Mill.) are frequent sub-dominants. Shrubs (e.g., Itea virginica L., Cephalanthus occidentalis L.) are generally clumped on raised microsites. Herbaceous groundcover is sparse.

Table 2.1. Importance values of tree species in natural floodplain forests of the Oklawaha River (control) and in Lake Oklawaha forests differing in depth of water. An indication of the frequency of stems of sprout origin is indicated for each species. Censused in May, 1987.

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SPECIES	COMMON NAME	SPROUTS
<hr/>		
<u>Taxodium distichum</u>	cypress	rare
<u>Nyssa sylvatica</u> var. <u>biflora</u>	swamp tupelo	rare
<u>Sabal palmetto</u>	cabbage palmetto	none
<u>Fraxinus</u> spp.	ash	many
<u>Acer rubrum</u>	maple	many
<u>Ulmus americana</u> var. <u>floridana</u>	American elm	few
<u>Ilex cassine</u>	dahoon holly	many
<u>Cornus foemina</u>	stillcornel dogwood	few
<u>Quercus laurifolia</u>	laurel oak	few
<u>Persea palustris</u>	swampbay	few
<u>Magnolia virginiana</u>	sweetbay	few
<u>Crataegus</u> spp.	hawthorn	few

---

\*(relative dominance + relative frequency + relative density) / 3

WATER LEVEL (cm)						
26 (control)	20	52	66	83	103	120
IMPORTANCE VALUE*						
13.5	18.8	15.6	23.2	32.6	62.0	67.5
7.3	3.7	7.0	6.3	10.6	24.2	17.5
3.9	7.4	4.3	4.9	0.0	1.9	15.0
44.7	40.5	47.1	44.8	49.4	8.4	
14.2	12.3	13.2	12.7	6.1	3.7	
5.8	6.6	2.7	2.2	1.3		
5.4	7.6	7.6	3.2			
0.8	1.7	2.5	2.7			
1.6	1.0					
0.3						
2.5						
0.3						

### Stem Mortality in Lake Oklawaha

Following impoundment of the floodplain forest, stem mortality rates increased with depth of inundation in a size (DBH) dependent fashion. Stem size-class distributions gradually changed with increasing water depth from large percentages in small size classes to more evenly distributed numbers of stems in all size classes (Figure 2.3). The fact that similar total numbers of trees were standing in water greater than 60 cm deep from 1972 to 1975 suggests that most tree mortality due to inundation had occurred between 1968 and 1972 (Table 2.2).

### Species Distributions in Lake Oklawaha

Tree species richness declined with increasing water depth in the impoundment (Table 2.1). Most species with low importance values in the natural forest became increasingly scarce in deeper water (e.g., sweetbay, dogwood, and elm); swamp tupelo and sabal palm, however, are important exceptions (see below).

Mortality rates of all species increased with depth of inundation; however, tree species differed in tolerance to standing water (Harms et al. 1980). Cypress, swamp tupelo and sabal palm were the only species that tolerated the deepest water (120 cm). Contrary to evidence from 1972 and 1975 that ash and maple would eventually die out in inundated portions of the impoundment, both species have maintained individuals in standing water 100 cm deep. Moreover, ash

Figure 2.3. Stem diameter size class distributions of trees with increasing depth of inundation and in control populations of Lake Oklawaha at three census dates. Years are given for census dates 3, 6 and 18 years following impoundment, respectively. Stem origin as a sprout (cross-hatch) or seedling (diagonal) was determined only in the last census.



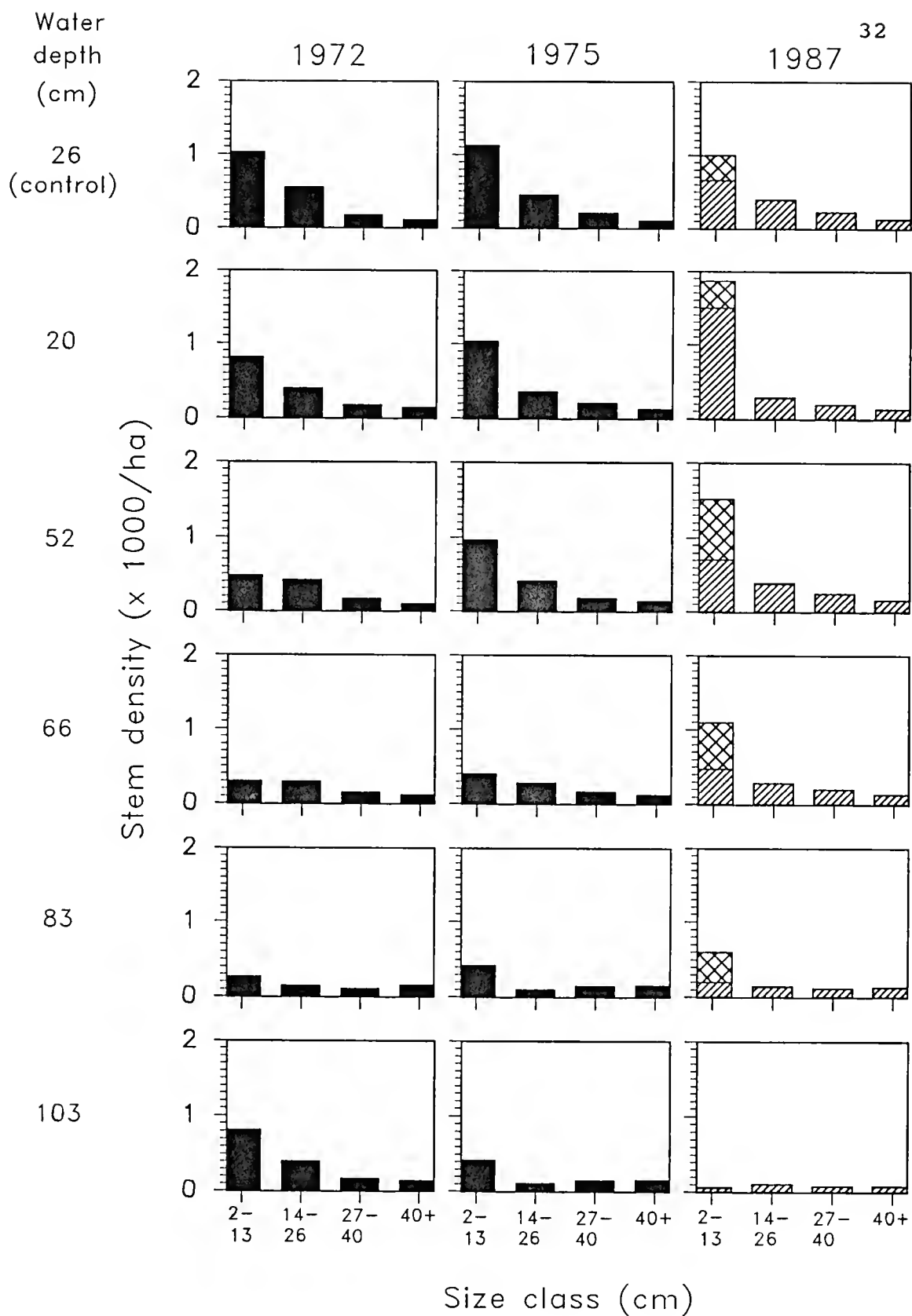


Table 2.2. Mean (SD) stem densities (stems/ha) of dominant tree species in natural floodplain forests of the Oklawaha River (control) and in Lake Oklawaha forests differing in depth of water. Significant differences between adjacent years of censuses are indicated by asterisk between columns ( $P < .05$ ).

WATER DEPTH (cm)	CYPRESS			ASH		
	1972	1975	1987	1972	1975	1987
26 control	120 (177)	106 (185)	114 (64)	1115 (396)	1108 (384)	1108 (697)
20	108 (70)	* 193 (159)	* 408 (295)	920 (469)	988 (478)	1298 (324)
52	63 (56)	100 (115)	190 (226)	763 (270)	* 1110 (462)	1550 (397)
66	78 (52)	83 (60)	185 (137)	428 (212)	* 530 (165)	* 1145 (364)
83	206 (174)	219 (174)	159 (137)	331 (108)	* 494 (214)	* 778 (569)
103	242 (152)	210 (153)	223 (254)	46 (72)	20 (31)	30 (60)

MAPLE			TUPELO			TOTAL		
1972	1975	1987	1972	1975	1987	1972	1975	1987
256 (203)	270 (214)	279 (250)	80 (104)	75 (96)	49 (45)	1902 (646)	1935 (646)	1771 (764)
180 * (115)	295 (334)	425 (317)	73 (95)	65 * (82)	13 (13)	1565 * (466)	1775 * (440)	2508 (858)
150 * (87)	20 (125)	320 (273)	25 (33)	15 (34)	30 (39)	1203 * (248)	1750 * (424)	2345 (570)
240 (177)	188 (162)	243 (306)	53 (104)	65 (88)	43 (58)	878 (234)	990 * (195)	1723 (385)
91 (104)	63 (75)	34 (50)	69 * (48)	25 (27)	31 (29)	709 (177)	860 (136)	1006 (503)
50 (57)	3 (8)	10 (32)	38 (44)	110 (173)	58 (68)	421 (265)	343 (214)	325 (30)

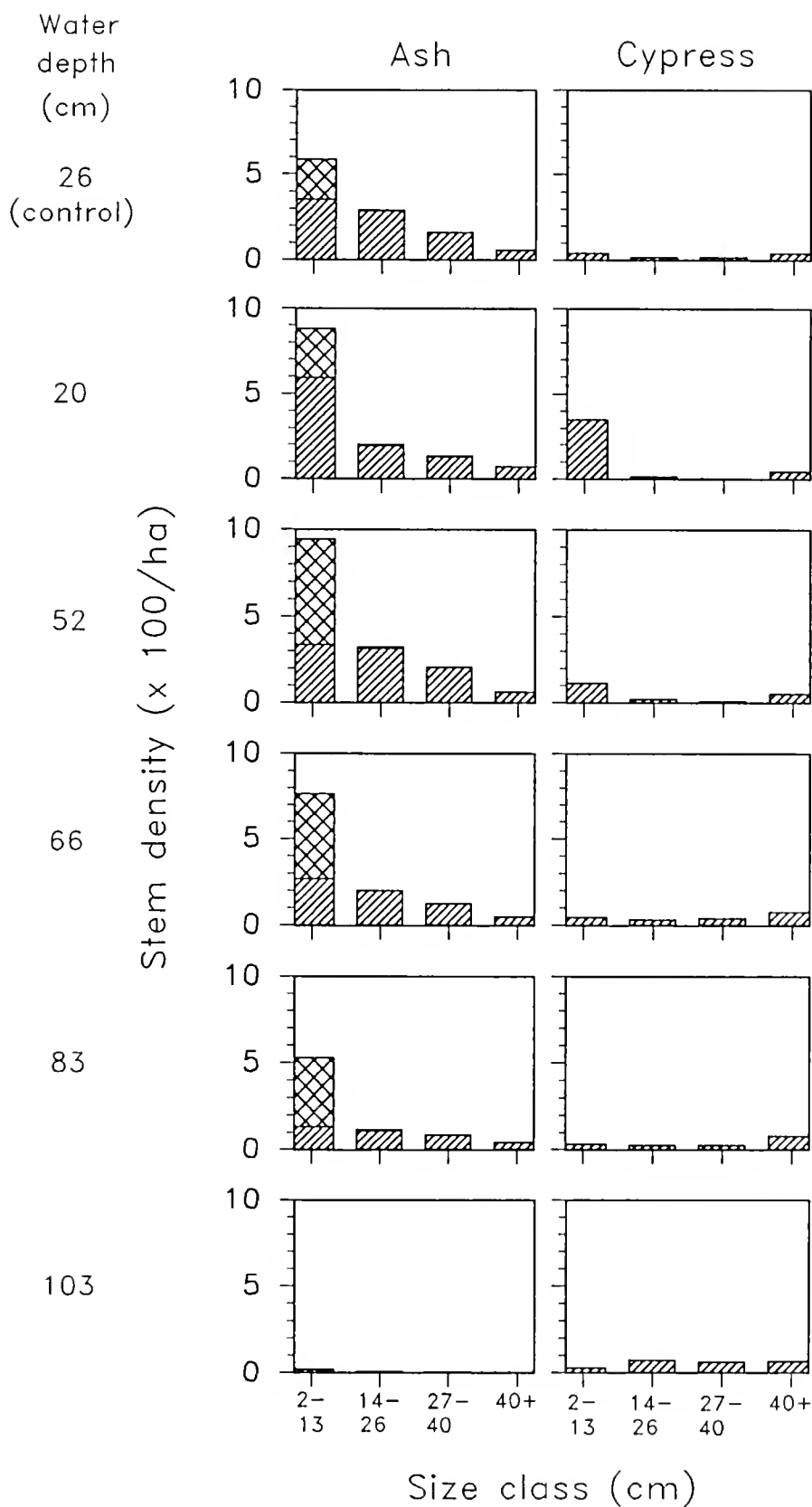
has maintained relative importance values in water depths up to about 80 cm similar to importance values in natural forests through the production of sprouts (Table 2.1, Figure 2.4). Several subdominant species (American elm, dahoon holly, and dogwood) not usually found growing in standing water are also able to maintain importance values in inundated areas similar to natural areas by sprouting (Table 2.1).

#### Recovery Following Impoundment

Although some trees continued to succumb under continuous deep inundation, recovery of stem density in moderately deep portions of the flooded forest was apparent by 1975. For example, stem densities between 2 and 13 cm DBH in water 83 cm deep increased from 272 stems/ha (SD=125; n=8) in 1972 to 431 stems/ha (SD=133; n=8) in 1975.

Overall, total live stem densities increased significantly from 1975 to 1987 in water depths up to 66 cm (Table 2.2). Numerous cypress and red maple seedlings were found in the shallowest areas of the impoundment adjacent to the Eureka Dam, which have had essentially natural river conditions since the second year of impoundment (Figure 2.2; see Johnson 1972 for details). The increases in stem densities by 1987 and the recovery of natural stem densities in standing water greater than 20 cm deep, however, were due to the sprouts produced by surviving individuals (Figure 2.3). Furthermore, the proportions of 2-13 cm DBH sprouts

Figure 2.4. Stem diameter size class distributions of ash and cypress trees with increasing depth of inundation and in control populations of Lake Oklawaha after 18 years of artificial impoundment. Stem origin indicated for sprouts (cross-hatch) and seedlings (diagonal).



increased with depth of inundation from 29% in natural populations up to 67% in 83 cm of water (Figure 2.3).

No trends were observed between increasing water depths and the proportions of stems that originated as sprouts in larger stem size classes. This may be due to short life spans of sprouts, or more likely there was inadequate time for sprouts to reach diameters greater than 13 cm following inundation.

The recovery of natural stem densities in the more deeply flooded areas of Lake Oklawaha was primarily a result of sprouts produced by ash (Table 2.2). In fact, ash stem densities increased in water depths between 66 and 83 cm, primarily due to sprouts, while the other dominant tree species at best only maintained densities similar to those measured in 1975. Although red maple stem densities did not increase significantly, high stem densities have been maintained by sprouts for 18 yr in greater water depths than where red maple is naturally found.

Ash and red maple tree stems that originated as sprouts are common in natural portions of this floodplain forest. One-third of stems from 2 to 13 cm DBH in control populations are sprouts from bases of both live and dead parent stems. Proportions of stems of sprout origin in larger size classes tend to be underestimated, because diameter growth of a stem can mask evidence of sprouting from a parent stem especially if only the sprout remains. Conservative esti-

mates of the proportions of stems of sprout origin in the larger size classes in natural populations are 2.3% for 14-26 cm DBH; 0.4% for 27-40 cm DBH; and less than 0.1% for greater than 40 cm DBH. Although we did not find a large percentage of sprouts in large size classes, these data indicate that stems of sprout origin can be long-lived and contribute to the maintenance of tree populations under natural conditions in these forests.

### Discussion

Based on censuses 3 and 7 years following impoundment of the Oklawaha River floodplain forest, Harms et al. (1980) predicted that bald cypress and swamp tupelo would "adapt to and be little affected by water depths of 0.6 m or less but the less tolerant ash and maple [would] eventually die out." In fact, after 18 years of impoundment, species richness has remained high in Lake Oklawaha. In addition to dominant tree species, many subdominant species have maintained importance values very similar to those in the adjacent natural floodplain forests in water depths up to 0.6 m.

The capacity for the tree species of the Oklawaha River floodplain to survive continuous inundation for 18 years was not evident from their distributions in natural systems. Bald cypress and swamp tupelo are commonly found along natural lake fringes, standing in water for long periods of



time. Red maple, ash, and the subdominant species, however, are usually restricted to seasonally inundated sites.

Capacities of wetland species to adapt physiologically and morphologically to inundation generally reflect patterns of flood tolerance (Gill 1970, Kozlowski 1984c). After 3 years of impoundment, Harms et al. (1980) found increased root mortality with increasing water depth. Cypress and swamp tupelo, however, had begun to develop new secondary root systems, whereas maple and ash had not.

In spite of high mortality rates of ash and maple following impoundment and other evidence that these species were relatively intolerant of long periods of inundation, a substantial number of individuals of these species, as well as other relatively flood-intolerant species, have persisted in Lake Oklawaha for 18 years. The mechanisms by which these individuals adapted to and tolerated continuous inundation are not clear. Intraspecific variation in physiological adjustments to the stress of inundation were likely to be involved (Keeley 1979, Sena Gomes and Kozlowski 1988, Chapter 4).

The trees in Lake Oklawaha had two maintenance patterns that allowed them to persist under the conditions of continuous and chronic stress imposed on the floodplain forest by the impoundment. Ash, red maple and many sub-dominant species effectively responded to artificial impoundment by regenerating vegetatively. Cypress and swamp tupelo toler-

ated continuously inundated conditions in this system, as well as other impounded areas, as long-lived stems, with no sexual or asexual regeneration (Eggler and Moore 1961, Conner et al. 1981).

The contrast between these two patterns is evident in the size class distributions of ash and cypress with increasing water depths (Figure 2.4). The longevities of cypress and swamp tupelo under continuous flooding determine the ability of these populations to recover by seeding in the event that water levels are lowered. The futures of ash and maple populations rely on the production of new sprouts to rejuvenate existing individuals. Both maintenance strategies are effective in sustaining populations capable of returning to natural regeneration patterns if water levels are lowered in the future.

Species with the ability to sprout are favored in stressful environments, particularly in many fire maintained communities (Abrahamson 1980, Malanson and Westman 1985), because sprouting is a regenerative mechanism in recovery from injury. Tree crowns snapped off by wind often resprout (Putz and Brokaw 1989). "Sprout forests" occur in many areas of the United States; these are primarily hardwood forests recovered from clearcutting in the early part of this century (Braun 1974). In fact, coppice management is an ancient hardwood forest management technique in Europe,

which is still in common use for the production of fuelwood (Auclair 1986).

Stress on the impounded floodplain forest in Lake Oklawaha, however, is much greater in both degree and duration than stress imposed on individuals by wind, fire, or logging. Even if continuously flooded plants have the capacity to adjust metabolically to anoxic conditions, growth rates never match those plants that are inundated periodically or by flowing water (Brown 1981). This is likely to be due to the adverse effects of flooding on photosynthesis and translocation of carbohydrates (Kozlowski 1984a).

It is because of this difference between degrees of stress to the individual that sprout production of the continuously inundated trees in Lake Oklawaha differs in function from the sprouting responses to a gap opening in a forest or loss of a stem to fire. Under these latter conditions, sprouting individuals can extend into unoccupied areas to exploit available resources (e.g., a gap) or simply restore balance to the root-to-shoot ratio (Kramer and Kozlowski 1979). In contrast, the release of sprouts under continuously flooded conditions serves as a survival mechanism that maintains the tree under long-term stress.

Novel and chronic perturbations to communities, such as infestation by viruses or insects, acid rain, climate change, and long-term flooding, dramatically shift communi-

ties to domination by species able to tolerate the situation. Vegetative reproduction serves as one mechanism by which plants can maintain themselves for long periods of time under chronically stressed conditions, perhaps until future conditions improve.

CHAPTER 3  
VEGETATIVE REGENERATION IN NORTH-CENTRAL  
FLORIDA WETLANDS

Introduction

Increases in vegetative regeneration in association with changing environmental conditions are common in plants (Bradshaw 1965, Abrahamson 1980). Two mechanisms exist by which such morphological variability can be expressed by a genotype (Bradshaw 1965): sprouting can be environmentally induced, or it can be an expression of a preadaptive trait that increases genet survival rates under new environmental conditions. Environmental cues for sprouting usually involve loss of aerial structures, as with, for example, sprouting responses to fire (Ohmann and Grigal 1981, Malanson and Westman 1985), grazing, wind damage (Putz et al. 1983), and logging (Braun 1974, Terwilliger and Ewel 1986). In contrast to sprouting in response to environmental cues, American beech (Fagus grandifolia Ehrh.) continuously produces root suckers throughout its geographical range. However, stems of root sucker origin were favored in the most severe climates because they were more tolerant of freezing early in the growing season than seedlings (Held 1983).

Many types of plant communities experience recurring disturbances differing in return frequency, intensity of stress induced, and predictability; these disturbances are usually integral to regeneration and competition processes. Longleaf pine forests of the southeastern Coastal Plain, for example, are considered to be disturbance-maintained communities with predictably frequent, low-intensity fires. When fire is excluded, species composition shifts from fire-tolerant species typical of these savannas toward fire-intolerant species of mixed-hardwood forests (Monk 1968). Black grama (Bouteloua eriopoda) dominated grasslands of southern New Mexico shifted to shrub-dominated communities when grazing pressure was intensified by domestic livestock (Schlesinger et al. 1990).

Sprout production, an expression of phenotypic plasticity, is adaptive in fluctuating environmental conditions; the rapidity of vegetative recovery following a destructive event gives sprouting plants an initial advantage over seedling establishment in reoccupying an area (e.g., Keeley 1981). Relative contributions of vegetative and sexual reproduction to perpetuation of populations often vary with the frequency, intensity, and seasonality of recurring stressful environmental conditions. For example, frequent low-intensity fires favor sprout production of chaparral shrubs (Keeley 1981), whereas intense summer fires in Pinus banksiana Lamb. forest communities destroy vegetative repro-

ductive structures, such as dormant buds on corms, favoring seedling establishment (Ohmann and Grigal 1981). Under less intense disturbances such as logging, sprout production is generally greater following disturbances that occur during the dormant season than during the early growing season (Belinger 1979, Harrington 1984). Seasonal fluctuations in carbohydrate and nitrogen reserve levels in roots are correlated with shoot growth vigor and may explain these patterns (Tromp 1983).

Disturbances such as fire, grazing, and logging are sources of physiological stress for plants. Partial removal of stems disrupts the root-to-shoot ratio, and consequently, the physiological state of the plant. If a vegetative response to stress is adaptive in communities subjected to such disruptive events, sprouting may also be adaptive under other less destructive stressful conditions. The observation that sprouts are more common in wetland than upland communities (personal observation) suggests that sprout production by wetland plants may be an adaptation to stress imposed by water level fluctuations.

North-central Florida wetland hydrologic regimes are analogous to fire regimes in that both have characteristic return frequencies and intensities that induce stress in plants. Depending on the relative position of wetlands in a drainage basin, depth, duration, and frequency of inundation will vary (Chapter 1). As fire intensity is determined by

temperature and speed of travel, the degree of anoxia and intensity of stress imposed on plants in wetlands is determined by the depth, duration, and frequency of inundation (Reddy et al. 1980).

Effects of hydrologic regime on relative contributions of vegetative and sexual reproduction to perpetuation of wetland tree populations should be evident from comparisons of population sprouting patterns among different wetlands. These patterns are likely to be significant for populations, communities, or both levels. Species-specific interactions with hydrologic regimes may differ. If, for instance, anoxia-induced stress affects mechanisms of apical dominance of red maple in a different manner than sweetbay (Magnolia virginiana L.), different sprout production patterns of these species would be expected where they co-occur. If, on the other hand, interactions of hydrologic regimes with mechanisms of apical dominance are not species-specific, consistent sprout production patterns within wetland communities would be expected, but a species' sprout production pattern might differ from wetland to wetland.

Sprouting patterns of trees in relation to inundation-related stress were investigated by describing the importance of sprout production and establishment (stems of sprout origin reaching at least 2 cm DBH) for common tree species occurring in wetlands of north-central Florida. These community and species-specific sprout patterns were



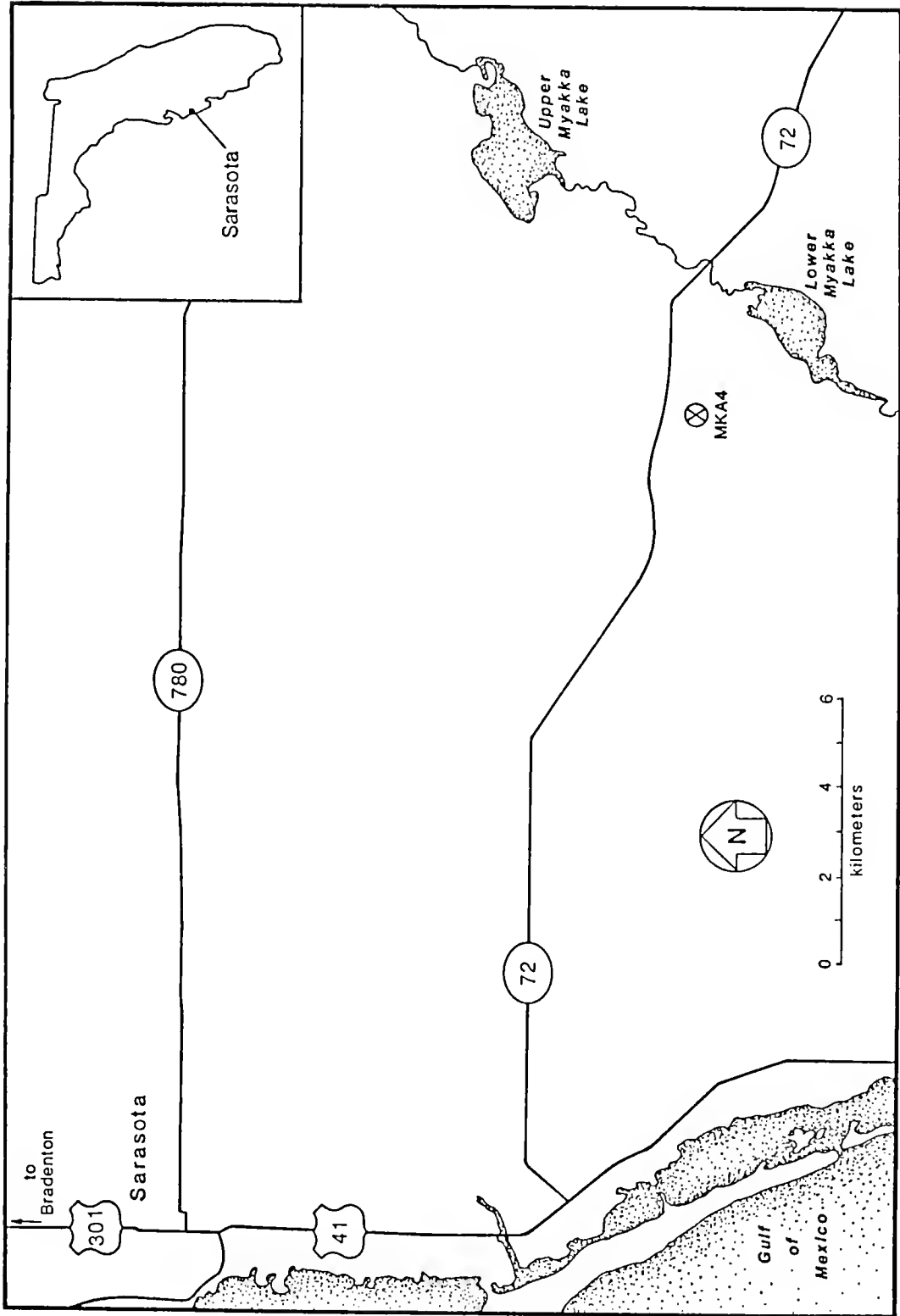
compared with hydrologic parameters to determine if increased stress induced by inundation increases rate of sprout production and establishment in natural wetlands.

### Site Descriptions

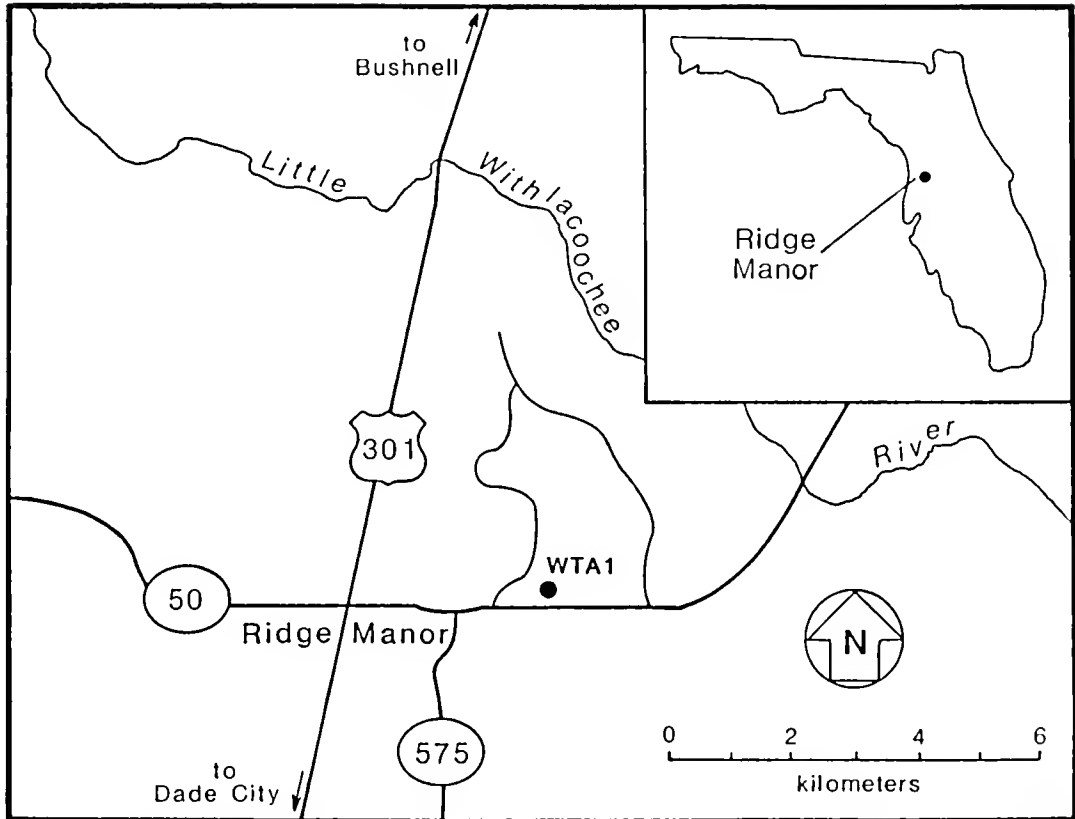
Twelve forested wetlands differing in both hydrologic regimes and species composition were selected throughout north-central Florida (Figure 3.1). Study sites were part of a larger study of common Florida plant communities conducted in cooperation with the Center for Wetlands, University of Florida, funded by the Florida Institute of Phosphate Research. All sites were at least partially logged during the first half of this century. Site selection was based on the presence of natural hydrologic regime (i.e., no indication of artificial drainage or inflow), the mature condition of the forest, and the long-term accessibility needed to monitor water level fluctuations over several years.

Seven of the study wetlands were hydrologically isolated from other wetlands (i.e., not connected by overland flow): two cypress domes (Figures 3.1A and 3.1B), three bayheads (Figures 3.1C and 3.1D), and two mixed-hardwood forests (Figures 3.1C and 3.1D). Water levels in these wetlands depend primarily on rain input and groundwater fluctuations. Water does not flow perceptibly in these

Figure 3.1. Natural forested wetland study locations: (A) Cypress Dome #1 (MKA4), Myakka River State Park, Sarasota County, (B) Cypress Dome #2 (WTA1), Withlacoochee State Forest, Hernando County, (C) Bayheads #1 and #2 (SMT2 and SMT1, respectively), Mixed Hardwoods #1 (OST2), and Slough (OST1), Orange County, (D) Bayhead #3 (HHP1) and Mixed Hardwoods #2 (HHP4), Highlands Hammock State Park, Highlands County, (E) Cypress Strand (OSC1), Osceola National Forest, Bradford County, (F) Lake Fringe (WSR2), Alachua County, (G) Floodplain (MPR1), Polk County, and (H) Groundwater fed stream (MMB2), Ocala National Forest, Marion County, Florida. Note: Location codes in parentheses cross-reference with study done in cooperation with the Center for Wetlands, University of Florida, Gainesville.

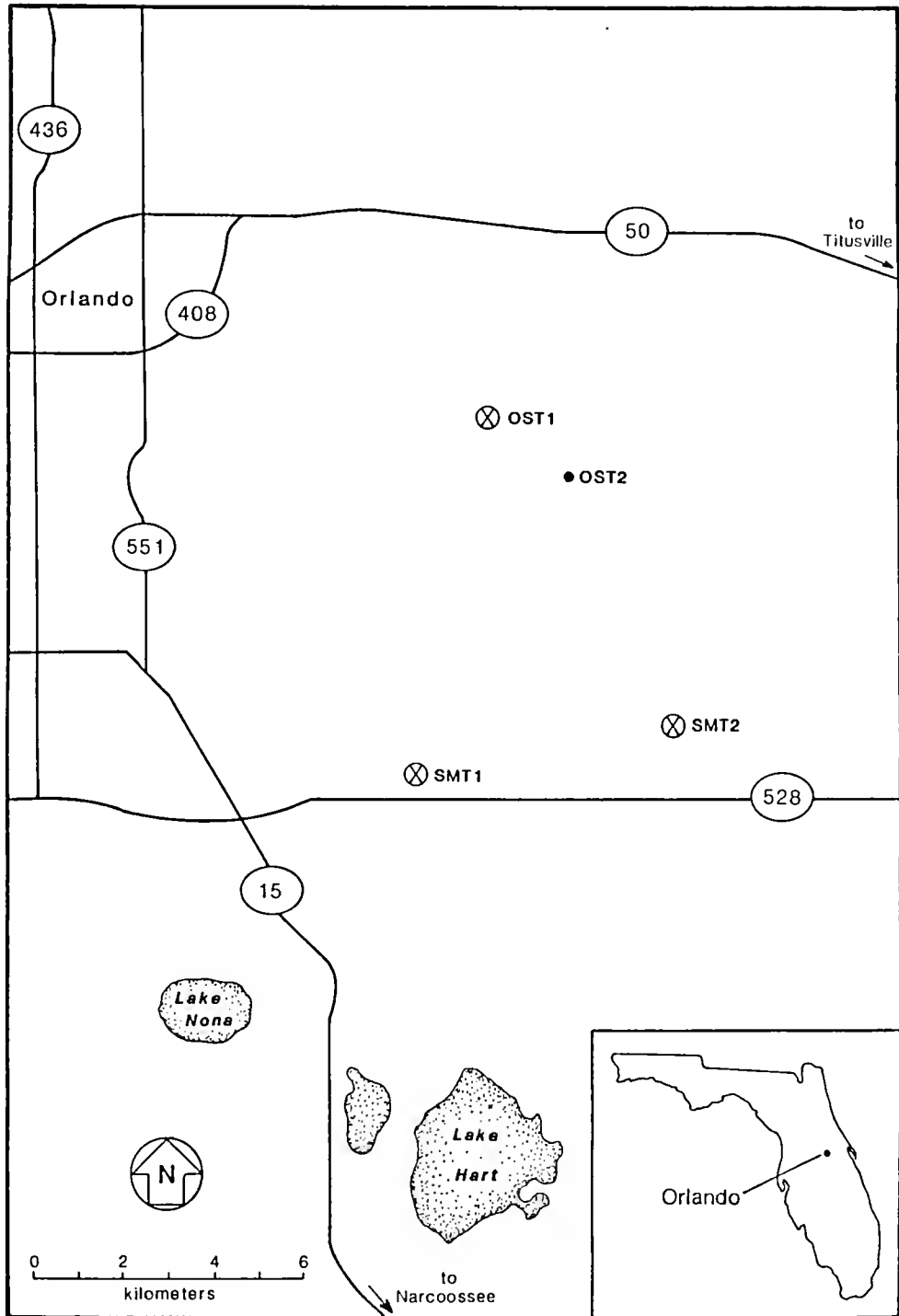


(A)



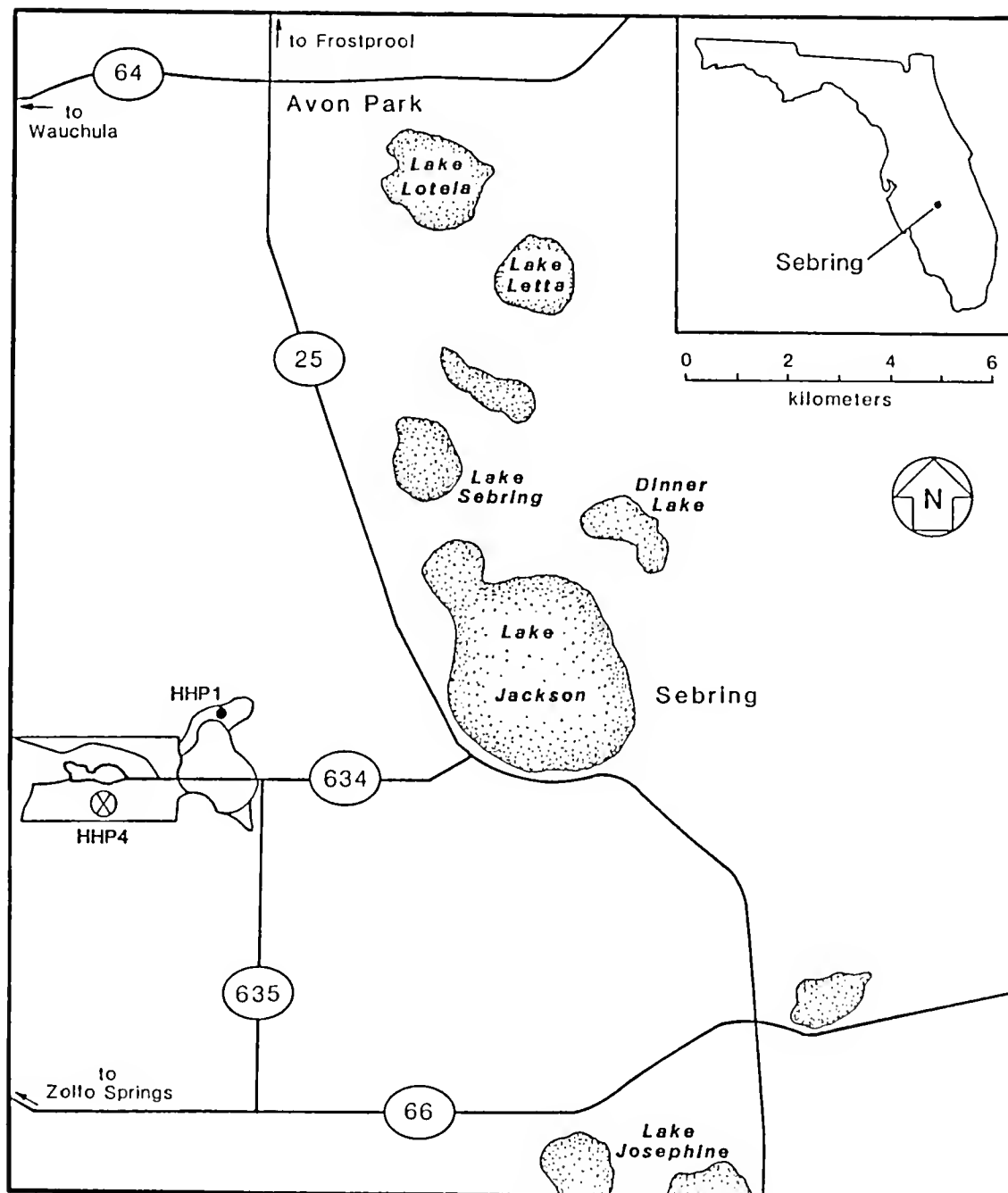
(B)

Figure 3.1--continued.



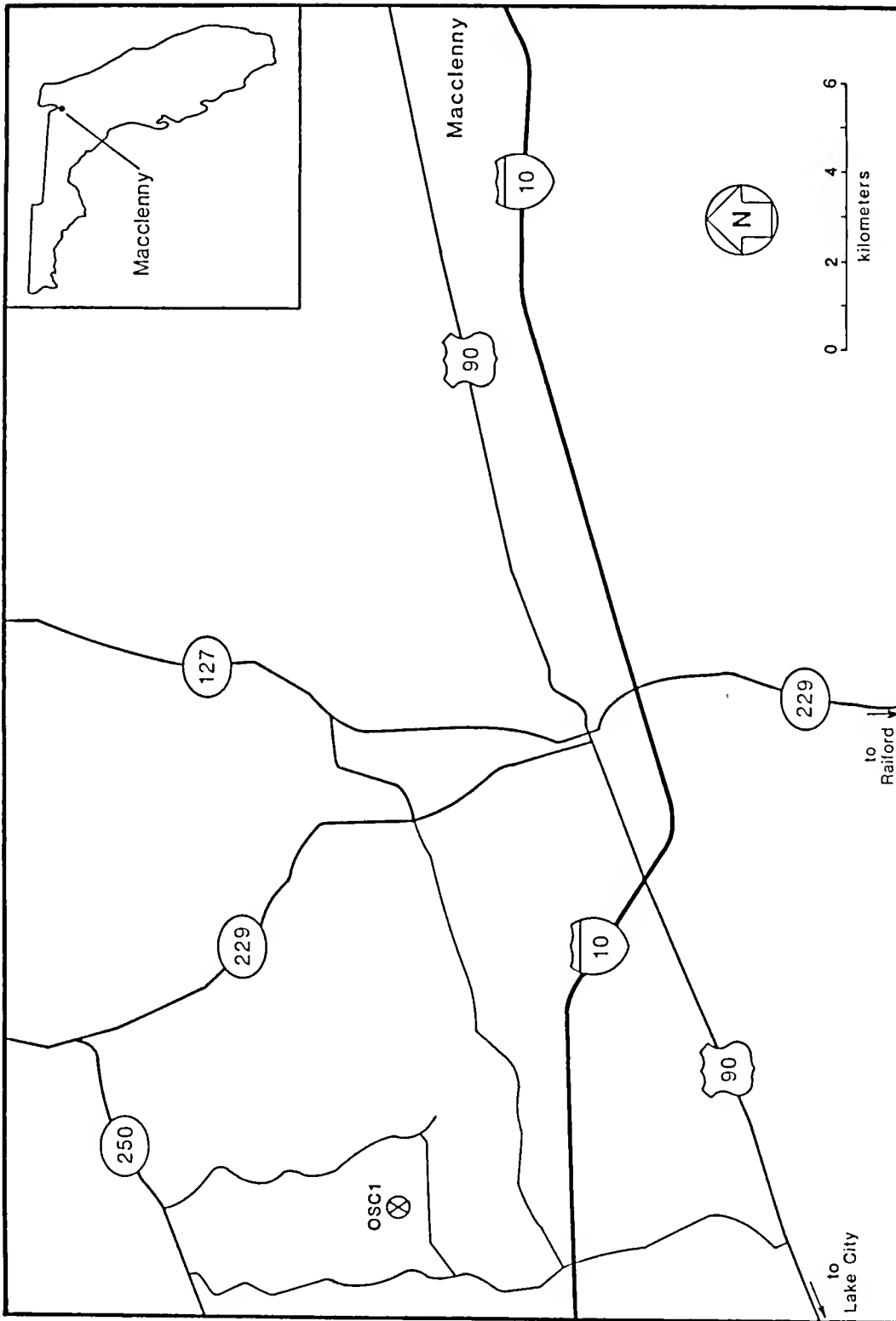
(C)

Figure 3.1--continued.



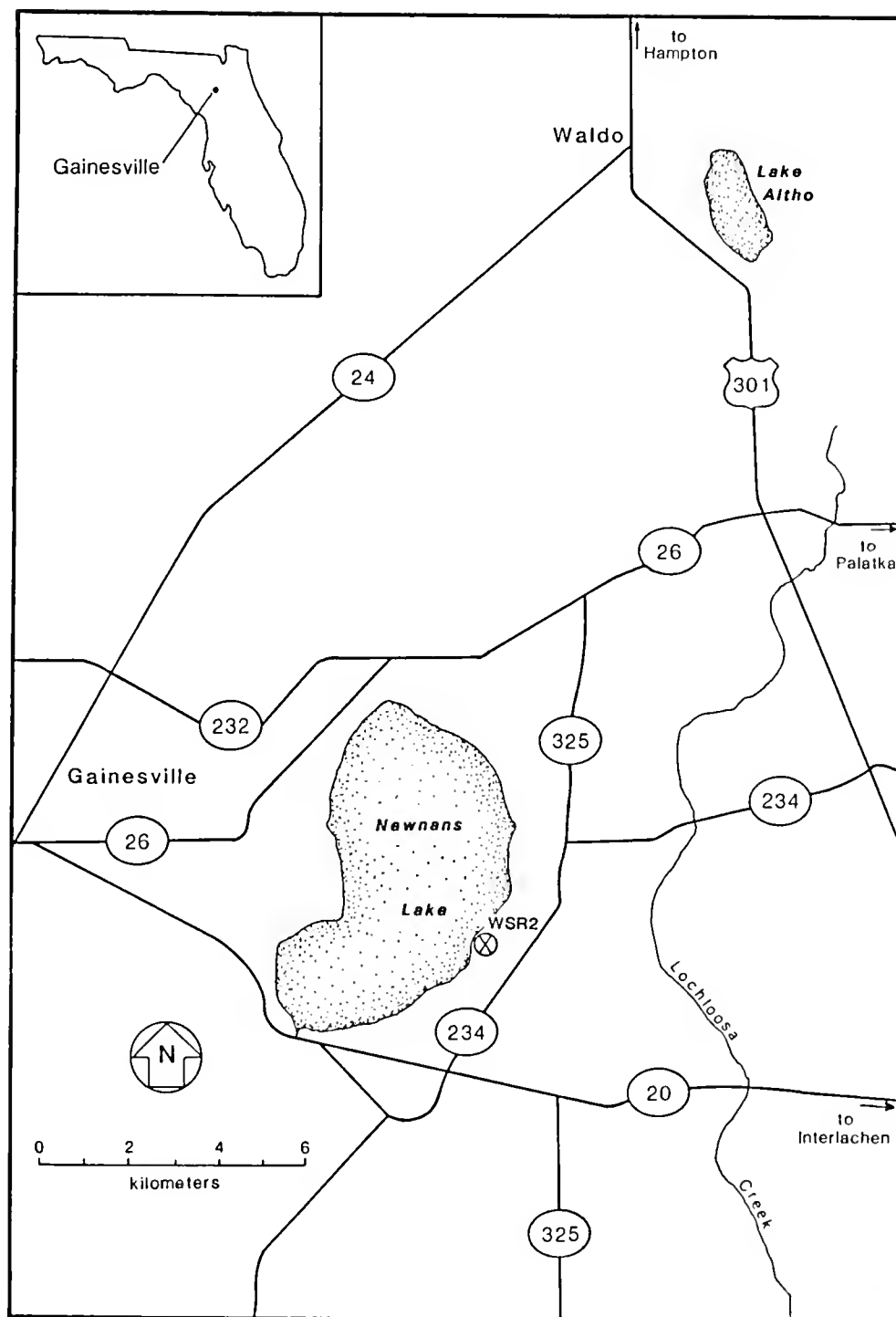
(D)

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(E)

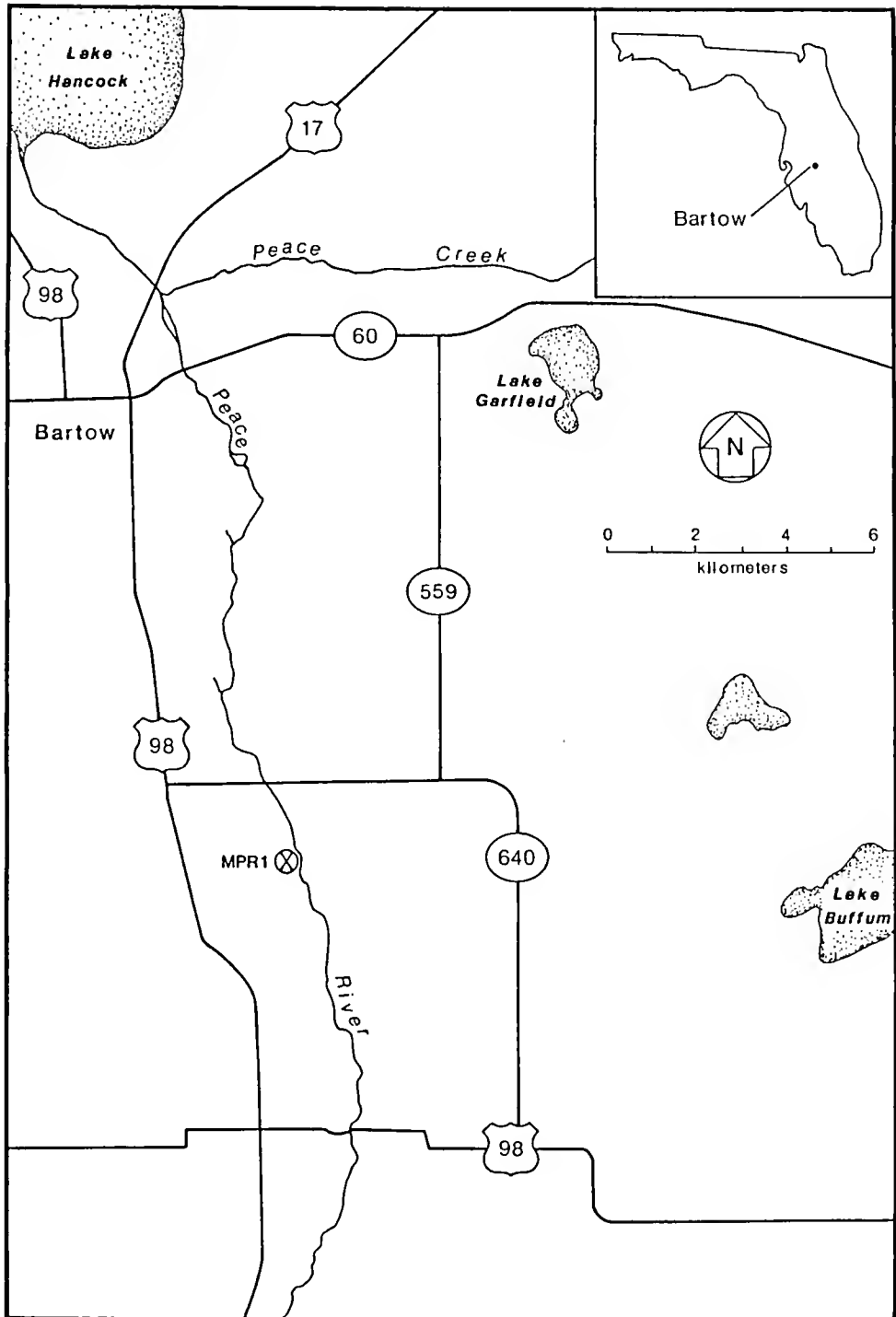
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(F)

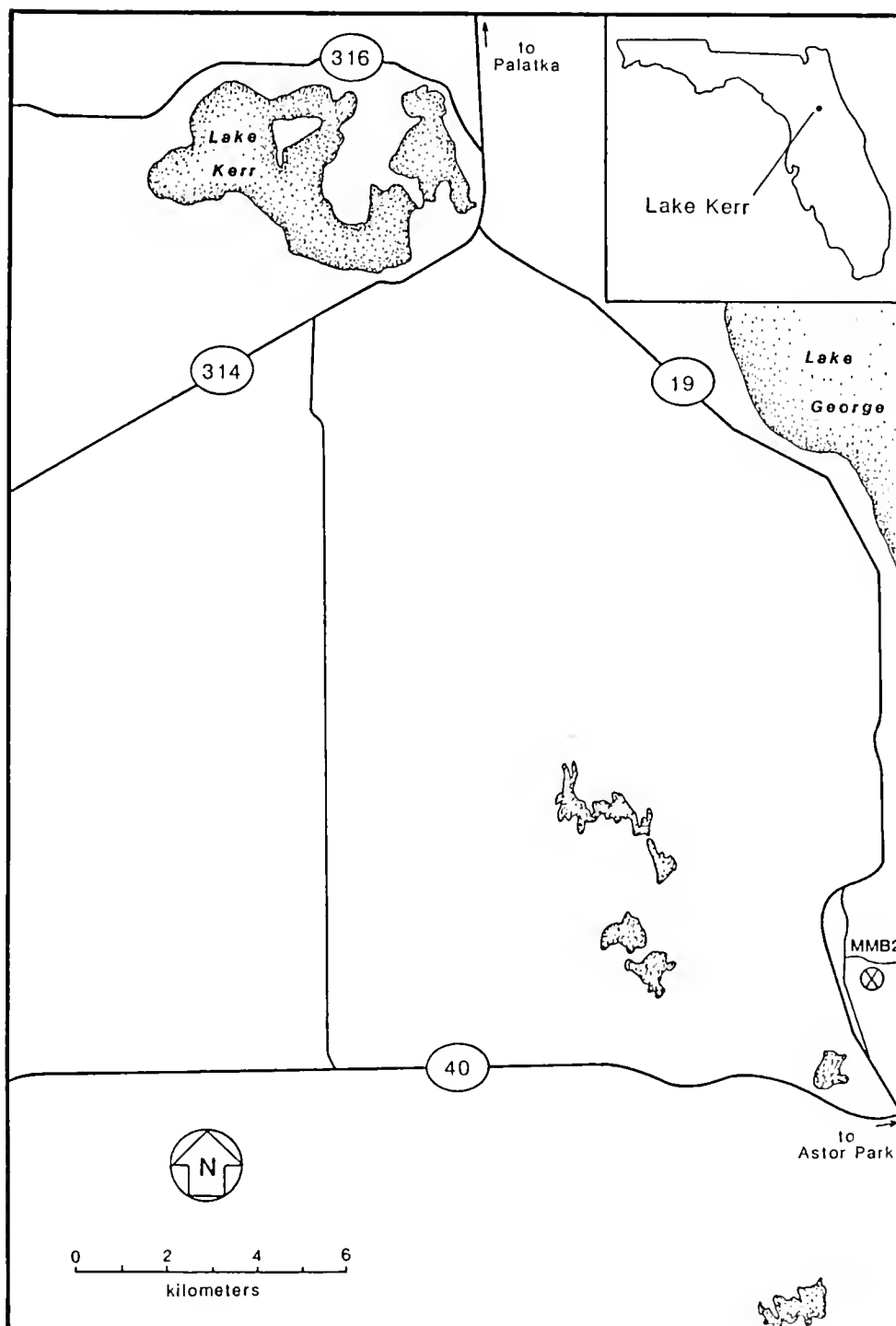
Figure 3.1--continued.





(G)

Figure 3.1--continued.



(H)

Figure 3.1--continued.

wetlands; water loss is through percolation and evapotranspiration. Consequently, water level fluctuations are relatively slow and there is often standing water in the summer and winter.

The remaining five wetlands were parts of overland drainage systems: a cypress strand (Figure 3.1E), a lake fringe forest (Figure 3.1F), a slough (Figure 3.1C), a floodplain forest (Figure 3.1G), and a forest along a groundwater fed stream (Figure 3.1H). These wetlands receive rain, groundwater, and overland flow in varying proportions. Water level fluctuations are usually seasonal, as in the isolated wetlands, but the rise and fall are more rapid and dramatic. Water flows through these systems, and, therefore, conditions associated with standing water (e.g., low nutrient availability, low reduction-oxidation potential) are less intense than in the hydrologically isolated wetlands.

## Methods

### Transect Establishment

Line transects were established across each wetland. Transects were surveyed from a random point in an upland association and were oriented perpendicular to the wetland boundary. Transects were divided into the component plant communities, generally uplands, wetland, and ecotones (areas of transition between uplands and wetland). This study used

information only from wetland portions of each transect as determined by ground surface profile and wetland plant distribution.

Delineation of forest community type followed Monk (1968) with the exception that mixed hardwood swamps in this study were further divided by hydrologic setting: hydrologically isolated mixed hardwoods, cypress strand, lake fringe, slough, floodplain, and groundwater-fed stream forests. Whereas no species-area relationships were determined for this study, it was determined that wetlands were adequately sampled because species composition of the forest types agreed with Monk (1968).

#### Ground Surface Profile

The physical profile of each transect was described by surveying relative elevation changes along each transect line. Elevation readings were taken every 2 m along the line except when microtopographic features (i.e., hummocks and stream channels) required that readings be taken at 0.1 m intervals. Organic soil depth was recorded at 4 m intervals by probing to mineral soil with a 1 cm diameter iron rod.

#### Ground Water Fluctuation

Piezometer wells were established at the midpoint or lowest elevation in each wetland. Wells consisted of 3.2-cm diameter schedule 40 PVC pipe, tipped with a PVC well screen. Each well was installed in an augered hole and soil

was backfilled around the pipe. Well depths varied from 1 to 4 m depending on location and proximity of groundwater to the soil surface. Wells were installed deeply enough to maintain contact with groundwater during dry periods and they extended above the ground high enough to remain visible during inundation. Groundwater levels were measured monthly from a reference mark of known relative elevation on the pipe.

Daily water levels were estimated from monthly measurements by non-linear interpolation using a spline technique (Michael Miller, unpublished BASIC computer program).

Hydrologic regimes were calculated for each wetland using measurement records from January 1986 to December 1987. For each elevation in the wetland (0.01 m increments) the following parameters were calculated to define the hydrologic regimes: average depth of inundation, percentage of time inundated during the two year period (duration), and number of times water rose above the elevation during the two year period (frequency). Hydroperiod calculations for the deepest point in the wetland were used for the community description.

### Soil Chemistry

Soil samples were collected from each well location. Three 5-cm diameter soil cores were taken from the top 10 cm of the soil profile within 1 m of the well. Samples from each well were mixed and subsampled for analysis. Analyses

were performed by the Institute of Food and Agricultural Science (IFAS) Extension Soil Testing Laboratory, University of Florida, Gainesville, Florida. Soils were analyzed for pH, organic matter content, and nutrients ( $\text{NH}_4$ ,  $\text{NO}_3$ , P, Ca, Mg, K, Fe, Mn, Zn, Cu, Cl, Na, and Al). Double acid extraction was used for P, K, Ca, Mg, Mn, Cu, and Zn, and samples analyzed by inductively coupled argon plasma (ICAP) spectroscopy.

### Tree Species Distributions

Species and diameter at breast height (DBH) were recorded for all woody stems > 2 cm DBH within 5 m of the transect. Euclidean coordinates of each stem were recorded. For stems situated on hummocks, hummock heights were also recorded.

Two sprouting conditions were noted for each stem: stem origin (parent stem or sprout) and the occurrence of a stem producing sprouts. Stem characterization was made in the same manner as for the Lake Oklawaha study (see Chapter 2).

Individual tree positions were used to describe ranges of environmental tolerance of tree species to hydrologic and soil conditions. Relative elevations and organic soil depths were interpolated for each tree from the physical profile. Frequency, depth, and duration of inundation were then determined for each tree based on measured water levels at each site.

### Data Analysis

Multiple regression analyses of environmental variables against arcsin square root transformed percentages of stems of sprout origin and of stems producing sprouts were performed using general linear models (PROC GLM, stepwise procedure, SAS 1985). Regression equations are reported in the text with regression coefficients and one standard error in parentheses. Categorical maximum likelihood analyses (PROC CATMOD, SAS 1985) regress  $\ln(P / 1-P)$  against independent parameters, where P is the probability of an event at different levels of the independent parameter. Maximum likelihood analyses were used to investigate the relationships between sprouting conditions of stems (stem origin and sprout production) to environmental parameters. Analysis summaries for results presented in tables are in the appendix.

### Results

#### Wetland Tree Species Distributions

Twenty-seven tree species were recorded in the 12 wetlands (Table 3.1). Most species were found in only one or two wetlands and had low relative importance values (less than 10). Eight species, however, were dominant or co-dominant species in several wetlands, and were used in both community and species level analyses of sprouting patterns.

Table 3.1. Diversity and importance values of trees in wetlands differing in hydrologic regime. Common species used in further analyses are denoted with asterisk.

HYDROLOGICALLY ISOLATED					
	Cypress Dome		Bayhead		
	#1	#2	#1	#2	#3
TRANSECT AREA (m <sup>2</sup> )	1420	1130	1700	2200	1200
SPECIES RICHNESS:	5	8	7	7	4
SHANNON-WEINER DIVERSITY (H):	0.06	0.18	0.55	0.62	0.30
EVENNESS (H / H <sub>max</sub> ):	0.08	0.20	0.65	0.73	0.50
SPECIES IMPORTANCE VALUES ((relative dominance + relative abundance) / 2):					
<u>Taxodium</u> spp. *	98.4	94.8	23.4	9.7	
<u>Ilex cassine</u> *	1.0	2.1	14.8	11.9	
<u>Nyssa sylvatica</u> var. <u>biflora</u> *	0.1	1.0	4.0	2.1	14.3
<u>Persea palustris</u> *	0.4		0.1	2.1	1.2
<u>Quercus virginiana</u>	0.1	0.7			
<u>Acer rubrum</u> *		0.3			
<u>Ilex opaca</u>		0.4			
<u>Quercus laurifolia</u>		0.5			
<u>Quercus nigra</u>		0.3			
<u>Magnolia virginiana</u> *			3.6	17.1	74.0
<u>Gordonia lasianthus</u> *			53.0	55.7	9.9



HYDROLOGI- CALLY ISOLATED		HYDROLOGICALLY CONNECTED				
Mixed Hardwoods		Cypress Strand	Lake Fringe	Slough	Flood- plain	Ground- water
#1	#2					
1050	950	2250	1650	2000	2600	2300
10	7	9	7	9	11	17
0.71	0.45	0.54	0.58	0.78	0.76	0.87
0.71	0.53	0.57	0.68	0.82	0.73	0.71
		53.5	41.0	12.2	9.5	
6.1		2.8		46.7	0.7	4.0
27.0	1.7	19.3	2.8	17.7		
2.5		0.6		2.7		7.4
41.1	6.4	0.2	3.0	5.4	12.3	3.9
0.3	2.8		14.3			2.9
					7.1	1.9
13.0		1.7		12.6		6.9
4.4		7.6		1.7		1.2

Table 3.1--continued.

HYDROLOGICALLY ISOLATED					
	Cypress Dome		Bayhead		
	#1	#2	#1	#2	#3
<u>Pinus serotina</u>				1.3	
<u>Pinus elliottii</u>			1.1		
<u>Fraxinus caroliniana</u> *					
<u>Liquidambar styraciflua</u>					
<u>Sabal palmetto</u>					
<u>Ulmus americana</u> var. <u>floridana</u>					
<u>Pinus palustris</u>					
<u>Cornus foemina</u>					
<u>Carpinus caroliniana</u>					
<u>Celtis laevigata</u>					
<u>Carya aquatica</u>					
<u>Chamaecyparis thyoides</u>					
<u>Morus rubra</u>					
<u>Pinus taeda</u>					
<u>Tilia caroliniana</u>					
CUMULATIVE IMPORTANCE VALUES:					
dicots	1.6	5.2	75.5	89.0	100.0
conifers and monocots	98.4	94.8	24.5	11.0	0.0

HYDROLOGI- CALLY ISOLATED		HYDROLOGICALLY CONNECTED				
Mixed Hardwoods		Cypress Strand	Lake Fringe	Slough	Flood- plain	Ground- water
#1	#2					
2.9				0.6		
2.4		13.9		0.4		0.2
	58.1		32.7		42.5	2.1
0.3	1.5				1.0	2.0
	26.8					49.7
	2.7		5.5		16.6	0.3
		4.0				
					1.7	1.6
					0.2	
					2.4	
					6.0	
						14.6
						0.2
						0.4
						0.8
94.7	73.2	28.6	59.0	86.8	90.5	35.1
5.3	26.8	71.4	41.0	13.2	9.5	64.9

Species richness and evenness of trees in hydrologically connected swamps generally were greater than in hydrologically isolated swamps (Table 3.1). Cypress domes and bayheads had the lowest species richness, with pond cypress dominant in cypress domes and broad-leaved, evergreen dicots, such as loblolly bay (Gordonia lasianthus (L.) Ellis.) and sweetbay, dominant in bayheads. Mixed-hardwood swamp forests generally had the greatest species richness and were dominated by one or more deciduous dicot tree species. Greater tree diversity in wetlands with water flow may be related to hydrologic conditions more conducive for seed dispersal; in addition, more variation in hydrologic conditions of connected wetlands than in isolated wetlands provides a wider range of establishment conditions.

#### Sprout Production by Dicot Tree Species

Stems producing basal sprouts (Table 3.2) and stems of sprout origin (Table 3.3) were found in all wetlands. Multiple regression analyses indicate that sprouting conditions of trees within wetland communities were not related to the importance values of the common tree species. The importance values of dicots versus other species of trees (i.e., conifers and monocots), however, were positively related to percentage of stems producing sprouts (Tables 3.1 and 3.2):

Table 3.2. Environmental condition significantly related to percentages of stems actively producing sprouts in natural forested wetlands.

	HYDROLOGICALLY ISOLATED				
	Cypress Dome		Bayhead		
	#1	#2	#1	#2	#3
Percentage of stems producing sprouts:	5.6	7.9	28.3	13.6	22.9
Iron (mg Fe / kg soil):	13.8	14.8	58.3	34.9	33.3

HYDROLOGI- CALLY ISOLATED		HYDROLOGICALLY CONNECTED				
Mixed Hardwoods		Cypress Strand	Lake Fringe	Slough	Flood- plain	Ground- water
#1	#2					
29.1	40.2	3.7	28.1	21.8	28.5	5.5
51.8	64.3	23.4	43.8	23.1	81.1	1.6

Table 3.3. Environmental conditions significantly related to percentages of stems of sprout origin in natural forested wetlands.

	HYDROLOGICALLY ISOLATED				
	Cypress Dome		Bayhead		
	#1	#2	#1	#2	#3
SPROUTING CONDITION:					
Percentage of stems of sprout origin	7.2	7.1	40.4	30.7	7.8
HYDROLOGIC REGIME:					
Average duration of inundation (% of 2 year record)	65.5	41.6	13.0	13.0	13.6
Average frequency of inundation (# of times in 2 years)	2.3	3.1	1.4	1.4	3.1
Average depth of inundation (cm)	14.2	10.1	1.3	0.7	0.7
STEM DISTRIBUTION:					
Percentage of stems on hummocks	0.9	6.6	65.7	29.8	0.7
SOIL CHARACTERISTICS (mg nutrient / kg soil):					
pH	4.1	4.3	3.8	3.6	3.7
Organic matter	3.7	6.4	18.6	26.7	14.0
Zinc (Zn)	1.1	1.5	2.9	3.0	1.8
Copper (Cu)	0.0	0.0	5.9	2.5	0.0
Chlorine (Cl)	4.6	8.8	31.6	15.2	19.7

HYDROLOGI- CALLY ISOLATED		HYDROLOGICALLY CONNECTED				
Mixed Hardwoods		Cypress Strand	Lake Fringe	Slough	Flood- plain	Ground- water
#1	#2					
22.4	10.9	4.4	27.1	22.6	34.5	5.2
41.6	83.2	61.5	47.8	48.1	8.9	5.4
3.3	2.2	3.5	3.4	3.6	7.3	0.1
5.9	18.9	8.0	16.0	8.1	3.1	1.7
40.6	1.7	5.1	0.0	41.7	0.2	0.6
4.5	4.1	3.7	5.6	4.4	6.0	5.6
18.1	21.3	13.7	4.4	26.0	1.3	50.0
4.1	3.5	0.8	1.2	3.1	6.0	0.3
3.2	0.0	0.0	0.0	2.0	0.0	0.0
45.5	19.4	9.5	0.0	26.7	4.4	83.9



percent producing sprouts =  $0.222 (\pm 0.068) + 0.004$   
 $(\pm 0.001)$  dicot importance value

( $R^2 = 0.57$ ,  $df = 1, 10$ ,  $P < .01$ ). Importance values of dicots in these wetlands were also positively related to percentage of stems of sprout origin (Tables 3.1 and 3.3):

percent sprout origin =  $0.234 (\pm 0.084) + 0.003$   
 $(\pm 0.001)$  dicot importance value

( $R^2 = 0.39$ ,  $df = 1, 10$ ,  $P = .03$ ).

#### Distribution of Stems Producing Sprouts

Percentages of stems in wetlands that were producing sprouts were not related to any combination of environmental parameters describing the hydrologic regime, topography, or stem distribution (e.g., stem density, basal area). This indicates that sprouts are equally likely to be produced under a wide variety of conditions in wetlands. Depth, duration, and frequency of inundation apparently did not stimulate or suppress sprout production. Light penetration and competition (indexed by stem densities and basal area) also were not correlated with sprout production.

Iron concentration was the only soil nutrient associated with the likelihood of basal lateral buds on stems breaking dormancy (Table 3.2):

$$\text{percent producing sprouts} = 0.222 (\pm 0.053) + 0.006 (\pm 0.001) \text{ Fe}$$

( $R^2 = 0.69$ ,  $df = 1, 10$ ,  $P < .01$ ). Soil iron concentrations are associated with buffering of the reduction-oxidation potential of flooded soils. It accounted for the greatest amount of variance in proportions of stems producing sprouts in these wetlands.

#### Distribution of Stems of Sprout Origin

In contrast to basal sprout production, percentages of stems of sprout origin in wetland communities are related to hydrologic regime parameters and percentage of stems situated on hummocks (Table 3.3):

$$\begin{aligned} \text{percent sprout origin} = & 0.263 (\pm 0.075) - 0.008 \\ & (\pm 0.002) \text{ duration} + 0.041 (\pm 0.016) \text{ frequency} + \\ & 0.031 (\pm 0.011) \text{ depth} + 0.007 (\pm 0.001) \text{ hummock} \end{aligned}$$

( $R^2 = 0.83$ ,  $df = 4, 7$ ,  $P < .01$ ). Largest percentages of stems of sprout origin were in wetlands with relatively high frequencies of water level fluctuations and deep average water depths but where sprouts could escape long periods of inundation on elevated microsites, the hummocks.

In addition to hydrologic regime and hummocks, several soil characteristics were significantly related to the

percentage of stems of sprout origin in wetland communities (Table 3.3):

$$\begin{aligned} \text{percent sprout origin} = & -0.281 (\pm 0.099) + 0.132 \\ & (\pm 0.022) \text{ pH} + 0.023 (\pm 0.010) \text{ Zn} + 0.084 \\ & (\pm 0.010) \text{ Cu} - 0.007 (\pm 0.001) \text{ Cl} + 0.007 \\ & (\pm 0.002) \text{ organic matter} \end{aligned}$$

( $R^2 = 0.96$ ,  $df = 5,6$ ,  $P < 0.01$ ). The pH is negatively correlated with reduction-oxidation potential, and, thus, high pH is associated with less reduced soils and better growing conditions. High organic matter is closely associated with hummock formation.

#### Sprouting Conditions of Common Wetland Tree Species

Stems producing sprouts and stems of sprout origin comprised a substantial portion of the 5154 stems censused in these 12 study wetlands (Table 3.4). Of the 27 species recorded, stems of 20 species were actively producing sprouts, whereas 15 species had stems at least 2 cm DBH that had originated as sprouts. All of the 8 most common wetland tree species both produced sprouts and had basal sprouts grow to at least 2 cm DBH.

The common tree species exhibited wide ranges of sprout production capacity and percentages of stems of sprout origin (Table 3.4). For example, production and establishment of sprouts by cypress were relatively infrequent when

Table 3.4. Overall sprouting characteristics of all common tree species individuals recorded in 3 or more natural study wetlands of north-central Florida.

SPECIES	COMMON NAME	N	NUMBER OF SITES	% STEMS PRODUCING SPROUTS	% STEMS ORIGINATED AS SPROUTS
<u>Acer rubrum</u>	red maple	234	6	42	20
<u>Fraxinus caroliniana</u>	pop ash	489	3	31	52
<u>Gordonia lasianthus</u>	loblolly bay	621	5	25	35
<u>Ilex cassine</u>	dahoon holly	397	6	21	49
<u>Magnolia virginiana</u>	sweetbay	542	6	25	12
<u>Nyssa sylvatica</u> var. <u>biflora</u>	swamp tupelo	422	6	5	10
<u>Persea palustris</u>	swampbay	104	5	19	13
<u>Taxodium</u> spp.	cypress	1672	8	5	4
others (19 species)		673	< 3 each	15	11
	Total	5154	12	16	18

compared with ash. In spite of this range of sprouting behavior, species importance values were not good predictors of sprouting in wetland communities.

Maximum likelihood analyses relating stem origin (Table 3.5) and sprout production (Table 3.6) of individual tree species to hydrologic parameters and hummock height revealed no consistent patterns. Red maple stems of sprout origin, for instance, were more common in situations with relatively shallow, more frequent and shorter inundation periods than stems that were not sprouts. In contrast, species such as swamp tupelo were more likely to have stems of sprout origin if the parent stems were on hummocks.

In spite of the suggestion of the maximum likelihood analyses that each species responded independently to environmental cues, if one species in a community had a relatively large percentage of stems of sprout origin, other species were also likely to have relatively more stems of sprout origin (Table 3.7). For example, in Bayhead #1, most species had relatively large percentages of stems of sprout origin, and, consequently, percentages that were high in comparison with sprouting of the same species in other communities. Percentages of stems of sprout origin of individual species can be ranked for every wetland where they occur. For instance, sweetbay occurred at seven sites (Table 3.7). Mixed hardwoods #1 had the lowest percentage of sweetbay stems of sprout origin, and the slough had the

Table 3.5. Mean (SD) hummock height and hydrologic conditions of stems by origin (P - parent; S - sprout) for common tree species in study wetlands. Significant maximum likelihood coefficients are indicated with asterisk between means ( $P < .05$ ). Note: Summaries of maximum likelihood analyses are in Appendix A.1.

SPECIES	NUMBER OF STEMS		HEIGHT OF HUMMOCK (cm)	
	P	S	P	S
<u>Acer rubrum</u>	187	47	4.0 (14.4)	9.4 (9.4)
<u>Fraxinus caroliana</u>	233	256	0.0 (0.0)	0.0 (0.0)
<u>Gordonia lasianthus</u>	406	215	8.3 (11.6)	8.3 (10.5)
<u>Ilex cassine</u>	204	193	7.9 (10.4)	11.0 (11.7)
<u>Magnolia virginiana</u>	479	63	2.1 (6.7)	* 5.2 (9.3)
<u>Nyssa sylvatica</u> var. <u>biflora</u>	380	42	2.0 (6.2)	* 8.8 (8.8)
<u>Persea palustris</u>	91	13	3.6 (7.5)	* 11.9 (12.8)
<u>Taxodium</u> spp	1613	59	0.7 (3.9)	0.6 (3.2)

DURATION OF INUNDATION (%)			FREQUENCY OF INUNDATION (per 2 yr)			DEPTH OF INUNDATION (cm)		
P		S	P		S	P		S
31.6	*	29.9	5.2	*	3.7	6.5	*	4.5
(32.6)		(31.8)	(4.0)		(2.7)	(7.1)		(5.5)
55.6		32.3	3.4		6.5	14.5		10.4
(33.6)		(30.4)	(3.6)		(4.8)	(9.4)		(10.3)
11.3		14.3	1.5		1.7	0.9		1.2
(18.5)		(21.3)	(1.9)		(1.9)	(2.1)		(2.1)
32.2		24.6	2.4		2.6	5.0		3.2
(33.0)		(28.2)	(2.0)		(2.3)	(7.6)		(5.9)
22.8		30.8	2.5	*	3.3	2.8	*	4.2
(27.5)		(28.4)	(2.0)		(2.0)	(5.3)		(6.5)
48.4		23.0	3.6		2.1	6.3		2.8
(29.1)		(28.9)	(1.8)		(2.2)	(5.7)		(5.6)
18.7		21.9	1.6		2.8	2.8		1.9
(29.3)		(23.1)	(2.0)		(2.3)	(6.0)		(2.2)
60.3	*	54.0	3.1		3.1	11.2		10.1
(23.3)		(16.8)	(1.8)		(1.4)	(7.8)		(4.4)

Table 3.6. Mean (SD) hummock height and hydrologic conditions of sprout production (NP - not producing sprouts; P - producing sprouts) for common tree species in study wetlands. Significant maximum likelihood coefficients are indicated with asterisk between means ( $P < .05$ ). Note: Summaries of maximum likelihood analyses are in Appendix A.2.

SPECIES	NUMBER OF STEMS		HEIGHT OF HUMMOCK (cm)	
	NP	P	NP	P
<u>Acer rubrum</u>	135	99	7.3 (17.1)	2.0 (5.7)
<u>Fraxinus carolina</u>	336	153	0.0 (0.0)	0.0 (0.0)
<u>Gordonia lasianthus</u>	465	156	7.8 (11.2)	9.8 (11.2)
<u>Ilex cassine</u>	314	83	9.0 * (11.1)	11.2 (11.4)
<u>Magnolia virginiana</u>	406	136	2.3 (7.1)	2.9 (7.1)
<u>Nyssa sylvatica</u> var. <u>biflora</u>	403	19	2.6 (6.7)	6.1 (7.9)
<u>Persea palustris</u>	84	20	4.5 (8.9)	5.3 (8.5)
<u>Taxodium</u> spp	1594	78	0.7 (3.8)	0.7 (4.4)



DURATION OF INUNDATION (%)		FREQUENCY OF INUNDATION (per 2 yr)		DEPTH OF INUNDATION (cm)	
NP	P	NP	P	NP	P
35.2 (33.9)	25.8 (29.5)	4.4 (3.6)	5.5 (4.1)	6.5 (7.4)	5.5 (6.1)
38.6 * (33.4)	53.8 (33.1)	5.7 (4.7)	4.4 (3.9)	11.4 * (10.2)	14.3 (9.3)
12.8 (19.9)	11.1 (18.5)	1.6 (2.0)	1.5 (1.7)	1.0 (2.1)	0.9 (2.1)
28.4 (30.6)	28.7 (32.4)	2.6 (2.2)	2.2 (1.9)	3.8 * (6.3)	5.1 (8.7)
20.1 (25.5)	34.3 (31.0)	2.4 (2.1)	3.2 (1.8)	2.3 (5.0)	4.8 (6.4)
46.2 (29.9)	37.0 (32.3)	3.5 (1.9)	3.2 (1.9)	6.0 (5.8)	5.1 (6.8)
18.7 (29.4)	20.7 (25.0)	1.6 (2.0)	* 2.6 (1.9)	2.8 (6.0)	2.2 (3.6)
60.7 * (22.8)	48.1 (26.1)	3.0 (1.6)	* 3.8 (3.3)	11.2 * (7.8)	9.9 (6.6)

Table 3.7. Percentages of stems on hummocks and stems of sprout origin of common dicotyledonous wetland trees species in study areas. Stem percentages are ranked (numbers in parentheses) across sites. See text for explanation of analysis.

HYDROLOGICALLY ISOLATED					
	Cypress Dome		Bayhead		
	#1	#2	#1	#2	#3
PERCENTAGE OF STEMS ON HUMMOCKS:	0.0 (1.5)	6.6 (8)	65.7 (12)	29.8 (9)	0.7 (5)
COMMON DICOT TREE SPECIES:					
<u>Acer rubrum</u>		0.0 (2)			
<u>Fraxinus caroliniana</u>					
<u>Gordonia lasianthus</u>			38.5 (7)	35.4 (5)	3.2 (1)
<u>Ilex cassine</u>	14.3 (1)	37.5 (4)	64.2 (8)	58.9 (7)	
<u>Magnolia virginiana</u>			21.7 (6)	9.6 (4)	9.2 (3)
<u>Nyssa sylvatica</u> var. <u>biflora</u>	0.0 (3)	0.0 (3)	66.7 (10)	53.3 (9)	0.0 (3)
<u>Persea palustris</u>	25.0 (7)		0.0 (1.5)	11.8 (4)	0.0 (1.5)
AVERAGE RANK FOR COMMUNITY	3.7 (6)	3.0 (4)	6.5 (12)	5.8 (9)	2.1 (1)

HYDROLOGI- CALLY ISOLATED		HYDROLOGICALLY CONNECTED				
Mixed Hardwoods		Cypress Strand	Lake Fringe	Slough	Flood- plain	Ground- water
#1	#2					
40.6 (10)	1.7 (6)	5.1 (7)	0.0 (1.5)	41.7 (11)	0.2 (3)	0.6 (4)
29.9 (7)	10.0 (4)	0.0 (2)	0.0 (2)	35.1 (8)	11.8 (5)	16.7 (6)
	14.8 (1)		50.9 (3)		75.6 (4)	25.0 (2)
22.2 (2)		36.0 (6)		25.0 (3)		33.3 (4)
41.2 (5)		21.7 (3)		43.8 (6)	100.0 (9)	17.4 (2)
3.0 (1)		14.3 (5)		23.9 (7)		3.6 (2)
17.9 (8)	0.0 (3)	1.7 (6)	0.0 (3)	11.6 (7)		
28.6 (8)		20.0 (5)		21.1 (6)	5.4 (3)	
5.2 (8)	2.7 (2.5)	4.5 (7)	2.7 (2.5)	6.2 (11)	6.0 (10)	3.2 (5)

highest percentage; sweetbay had rank 1 at Mixed hardwoods #1 and rank 7 at the slough. Community averages of these ranks of relative sprouting success were positively correlated with ranked percentages of stems that occurred on hummocks (Kendall Coefficient of Rank Correlation = 0.51,  $P < .05$ , Table 3.7).

### Discussion

Basal sprouts of trees in north-central Florida wetlands are widely distributed across both species and hydrologic regimes. As described for other dicot-dominated vegetation (see Abrahamson 1980, Davis unpublished data), a large percentage of these wetland tree species (87%) was capable of reproducing vegetatively. Forty-four percent of the wetland tree species, principally the common dicots, had individuals of sprout origin  $> 2$  cm DBH.

Sprouts are produced throughout a wide hydrologic range (i.e., depth, duration, frequency) in north-central Florida wetlands. Whereas stems of sprout origin were generally more common on hummocks in wetlands with brief but frequent periods of deep inundation, trees producing sprouts were found in all hydrologic settings.

These results indicate that, unlike sprouting in response to disturbances such as fire, sprout production is neither in response to nor adversely affected by water level fluctuations. Establishment of sprouts as large diameter

stems depends upon surviving periods of inundation; sprouts on parent stems situated on hummocks are best able to avoid the adverse effects of inundation.

Two lines of evidence support the hypothesis that importance of sprouts in north-central Florida wetlands is primarily a community rather than a species-specific level phenomenon. First, significant relationships between certain soil and hydrologic parameters and the percentage of stems of sprout origin suggest better sprout success where establishment conditions are most conducive for growth (i.e., highly aerated substrate). Moreover, consistent sprout success of many species within a community indicates a common response to environmental conditions, particularly the presence of hummocks. The lack of consistent patterns of sprout production and growth in relation to environmental conditions for the individual species reflects the incongruency of their environmental tolerance ranges.

Most wetland trees are capable of producing sprouts throughout their natural range of hydrologic conditions, as well as under altered regimes (see Chapter 2). This indicates that the primary mechanism by which sprout production is expressed, and becomes important, is as an endogenously produced trait that is adaptive under certain environmental conditions.

Plants cannot respond to rapidly changing environmental conditions, such as fluctuating water levels, by directly

adaptive genetic changes (Bradshaw 1965). Continual sprout production in a fluctuating environment would be advantageous for vegetative reproduction because of the rapidity of environmental changes; sprouts produced in response to inundation would not be likely to survive the event and therefore would not be adaptive. Continuous sprout production allows the plant to be in the appropriate regenerative state before the critical environmental changes occur (Bradshaw 1965); sprout survival is increased by growth prior to inundation, before physiological stress and the consequent suppression of growth.

Sprout-producing species have the potential to regenerate regardless of the hydrologic state of the wetland. Whereas sprouts are susceptible to the effects of flooding, tree seedling establishment in wetlands is rare (Huenneke and Sharitz 1986, Brandt and Ewel 1989) primarily due to reduced metabolic rates following submersion (Pereira and Kozlowski 1977). Under these circumstances, increased longevity of a sprouting individual potentially increases fitness; the likelihood of being present to produce seeds increases when environmental conditions allow seed regeneration (Abrahamson 1980), for example, when water levels remain low following a good period of seed production.

Thirty percent of the 2900 stems of the 7 common dicot species recorded in this study of wetlands originated as sprouts; given the methods used to determine stem origin, I

believe this estimate is conservative. Such high percentages of sprout-originated stems among the most common species should have important repercussions for the stability of communities and for rates of species succession (see Chapter 5). Indeed, based on community diversity and structural complexity, Monk (1968) ranked dicot-dominated bayheads and mixed hardwood swamps in north-central Florida as seral stages replacing cypress domes. Although cypress domes are not obligatory for the formation of mixed hardwood swamps, in the absence of fire, particularly following disturbance (i.e., logging, drainage), cypress is not likely to replace itself and cypress dominated systems are then encroached upon by dicots (Rochow 1985, Brandt and Ewel 1989).

Abrahamson (1980) describes a general pattern of shifting from seed reproduction to vegetative reproduction with succession. The propensity of dicots to continually produce advance regeneration in the form of sprouts, even when there is no mechanical injury to the tree, that are capable of surviving a range of environmental conditions is an obvious advantage over conifers: the possibility of species turnover is much reduced. Increased vegetative reproduction in late successional forests is likely to be a consequence of this advantage and contributes to the unlikelihood of conifers naturally replacing a hardwood forest.

In conclusion, establishment of stems by sprouting is an important mechanism of regeneration in north-central Florida wetlands, especially for dicots capable of continually producing basal sprouts. Sprout survival of all species appears to be determined by the ability to avoid inundation, and is facilitated by the presence of hummocks on which parent stems are situated. Successful vegetative regeneration is likely to be a contributing factor in reduced species turnover rates and stabilization of mature community structure.



## CHAPTER 4 APICAL DOMINANCE: MECHANISMS AND ECOLOGICAL SIGNIFICANCE

### Introduction

Interactions between specific environmental conditions and mechanisms of apical dominance need to be understood in order to predict sprout production patterns. Whereas the temptation exists to infer process and mechanism from patterns, the complexity of ecological systems often undermines such simplistic approaches. Such is the case for sprouting patterns in wetlands of north-central Florida; inference of mechanisms of apical dominance from sprout distributions in Lake Oklawaha would lead to different conclusions than inferences from distributions in natural wetlands.

Sprout distributions in natural wetlands suggest that there is little interaction between inundation and sprout initiation, insofar as the capacity to produce sprouts is a species-specific trait and is independent of hydrologic conditions. Avoidance of submersion, however, is the key to sprout survival (Chapter 3). Observed increases in proportions of stems of sprout origin with increase in water depth in Lake Oklawaha suggest that increased anoxia-induced stress stimulates sprout production. Inundation of plant roots leads to a sequence of responses that could affect

apical dominance of sprout initiation; results of studies of the artificially impounded floodplain forest in Lake Oklawaha and natural forested wetlands do not clearly indicate the nature of that relationship.

Sprout production as a consequence of relaxed apical dominance could be induced by a number of environmental stimuli resulting both directly and indirectly from flooding, such as altered root-to-shoot ratios, light on stems, hormone balance, or plant water status. An initial result of flooding is generally high root mortality (Harms et al. 1980). A root system with many damaged roots cannot support a large amount of foliage, and thus flooding is often followed by crown dieback. There is evidence for this in the sparse foliage of the floodplain forest canopies 18 years after impoundment in Lake Oklawaha. Loss of leaf area would result in the reduction of auxin production sites. The theory of apical dominance by hormonal control (e.g., Rubenstein and Nagao 1976) predicts that the consequent reduction in auxin concentrations would reduce apical dominance and initiation of sprout growth could occur. Whereas this is feasible, there is some evidence to suggest that flooded plant auxin concentrations increase due to reduced basipetal movement and reduced auxin breakdown rates; in addition, cytokinin production is reduced following root death (Reid and Bradford 1984). The altered auxin and cytokinin concentration balance presumably enforces apical dominance

(Salisbury and Ross 1985). Indirect effects of foliage loss are increased light penetration and temperature of the stems. Epicormic branching is thought to be stimulated by the increased light reaching stems when canopies are opened (Trimble and Smith 1970) or the associated heating of stems.

Although crown loss and thus light penetration into the forest often increase with depth of inundation, it is unclear whether these indirect effects of flooding initiated sprout production in Lake Oklawaha. Foliage stress and dieback do not occur in swamps with natural water level fluctuations. Proportions of stems of sprout origin in natural swamps are not related to stem density, which suggests that there is no relationship with canopy closure. Furthermore, there is apparently no direct effect of flooding on sprout production in natural swamps; sprout production is not related to any of the measured hydrological parameters (Chapter 3).

In contrast with the hormonal explanation of apical dominance, the theory of apical dominance by lateral bud sink strength for plant water predicts initiation of lateral bud growth when their relative sink strength for available xylem water is greater than apical bud sink strength (McIntyre 1987). These conditions may exist following inundation when stomata close, a common initial response to flooding (Gill 1970). With stomatal closure, transpiration rates are reduced and stem xylem water potential remains

high (Pereira and Kozlowski 1977, Reid and Bradford 1984). These conditions are necessary to initiate sprout growth by increasing relative sink strength of lateral buds for water.

To the extent that the apical dominance theory of bud sink strength applies, species that differ in the duration of time required to resume normal plant water relations following inundation are expected to have different periods of time during which apical dominance is reduced by flooding. Red maple (Acer rubrum L.) and swamp tupelo (Nyssa sylvatica var. biflora (Walt.) Sarg.) are common in many types of forested wetlands in north-central Florida. Swamp tupelo is very flood tolerant (Eggler and Moore 1961, Harms 1973) and is commonly found in standing water under natural conditions. Red maple grows more often in areas that drain frequently; only scattered individuals can be found growing naturally in standing water. In Lake Oklawaha and in natural wetlands, red maples are prolific sprout producers whereas swamp tupelo sprouts are rare. For these two species under these conditions, the degree of flood tolerance is negatively associated with sprout production. I hypothesize that flood tolerant species like swamp tupelo recover normal transpiration rates more rapidly following inundation than less flood tolerant species, like red maple. A longer period of inhibited transpiration of red maple trees would allow lateral buds to initiate growth, thus increasing sprout production rates.

The experimental portion of my research tested aspects of both the hormonal and plant water relation theories of apical dominance as mechanisms controlling sprout production that interact with anoxia-induced stress in swamps. I conducted a field experiment using mature red maple trees to test the hypothesis that the sprouting response of flooded trees is due to altered shoot-to-root ratios. Sprout production was predicted to increase with a decrease of the shoot-to-root ratio and to decrease with decreased light and temperature levels of the tree trunks. A shadehouse experiment using one-year old red maple and swamp tupelo seedlings tested effects of transpiration rates inhibited by flooding and application of a chemical anti-transpirant on rates of sprout production and growth. I predicted that sprout production of seedlings grown under various soil moisture conditions would increase when transpiration rates were reduced. In the final experiment, red maple and swamp tupelo seedlings were placed in humidity controlled chambers to test the effects of altered transpiration rates on sprout production and growth. Again, I predicted that sprout production by seedlings would increase when transpiration rates were reduced due to increased water sink strength of lateral buds relative to apical buds.

## Methods

### Red Maple Field Experiment

An experiment with mature red maple (Acer rubrum L.) trees was conducted in Withlacoochee State Forest, Sumter County, Florida (Figure 4.1). The swamp had a sparse canopy dominated by red maple trees interspersed throughout with Carolina willow (Salix caroliniana Michx.). Most of the red maple crowns were columnar and relatively narrow in diameter. The forest canopy was open with high light penetration at ground level. The groundcover, nearly 100% sawgrass (Cladium jamaicense Crantz), was fairly dense except directly under trees > 8-10 cm diameter at breast height (DBH) where it was shaded out.

The study was conducted using 80 single-stemmed red maples between 2 and 10 cm DBH within a 40 x 100 m plot. All basal stem sprouts below breast height were counted and removed; small sprouts were pulled off and sprouts too large to break were clipped. Each stem was mapped, measured for DBH, and permanently tagged. Many of these trees were established on elevated microsites, the sawgrass bases, and had roots exposed above the ground surface.

Treatments consisted of partial canopy removal, partial root system removal, and decreased light levels on the lower portion of the stem. The canopy removal treatment consisted of cutting about 1/2 of the leaf-bearing branches from the

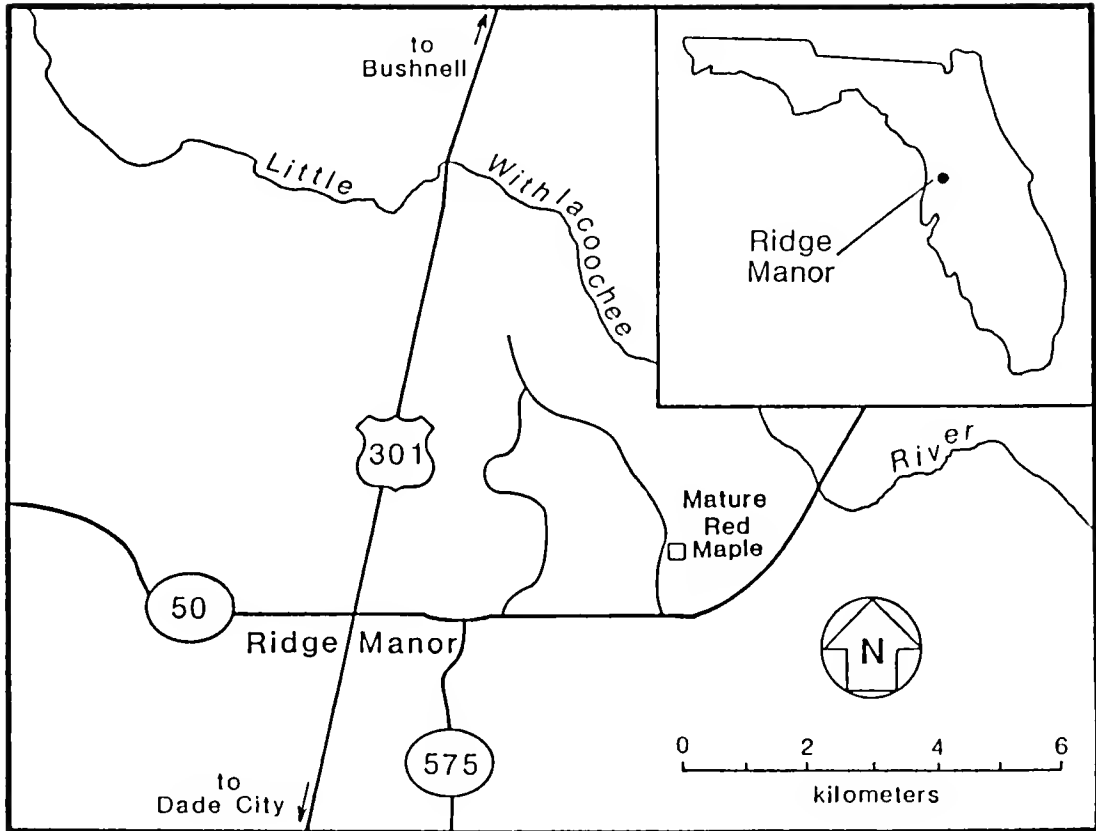


Figure 4.1. Site location of red maple field experiment in Withlacoochee State Forest, Hernando County, Florida.

upper portion of the canopy. One half of the root system was removed by severing roots around 1/2 the stem with a 45-cm long shovel, assuming that roots were uniformly distributed around the stems. Light levels were reduced on the lower portion of the stems (i.e., below breast height) by hanging an opaque black polyethylene tarp loosely around the stem from the lower limbs of the tree and holding it away from the stem by staking out the corners (Figure 4.2).

Treatments were applied on 25 May 1988, and treatment effects on sprout production were recorded at the end of the growing season (21 October 1988) and again the next spring (1 May 1989). I recorded numbers of basal stem sprouts on each stem; conditions of the parent stem and sprouts were noted as well. Relative depth of water at the base of each stem was measured in October 1988.

Each tree was considered to be an independent sampling unit. The experimental design was a completely randomized 3-factorial ( $2 \times 2 \times 2$ ) G-test (Sokal and Rohlf 1981) with 40 replicates of each main effect and 10 replicates for each of the 8 treatment combinations. Relationships of sprout production with location in the swamp and water depth were investigated using regression analyses.

#### Shadehouse Experiment

Two tree species that are common in swamps of north-central Florida with different hydrologic regimes were chosen for the shadehouse experiment. The species, red



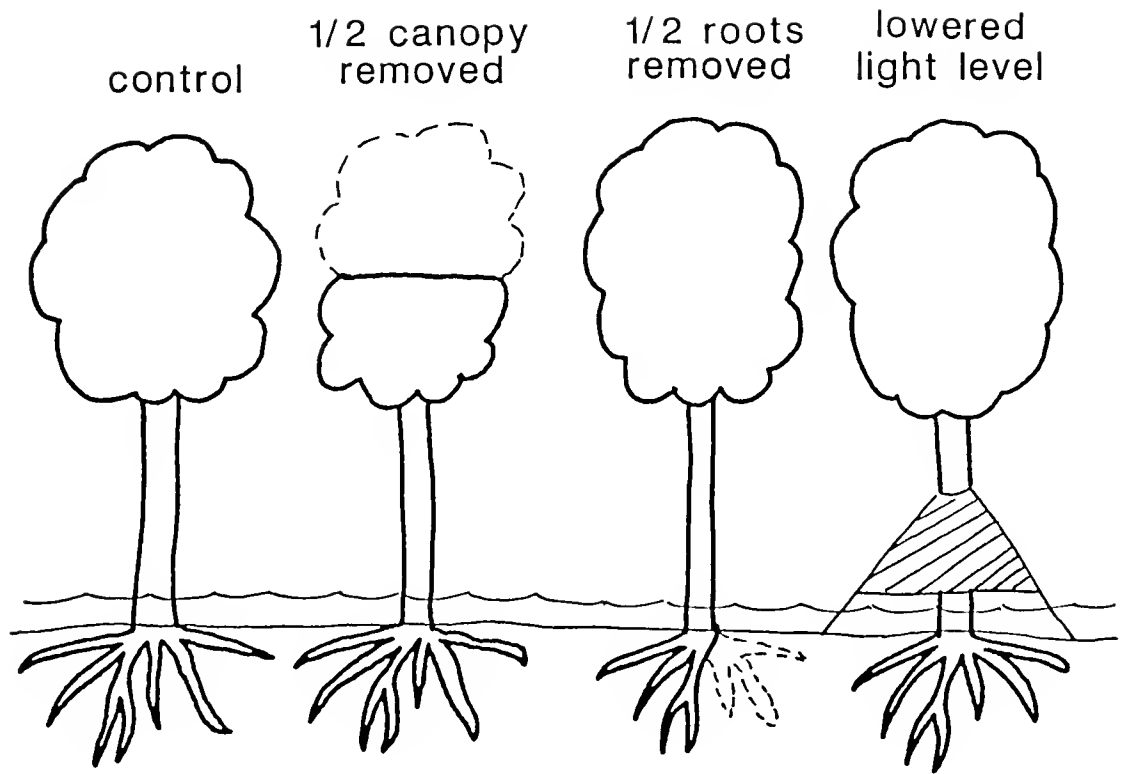


Figure 4.2. Experimental treatments in red maple field experiment.

maple and swamp tupelo, differ in their propensity to sprout: red maple often produces numerous basal sprouts, whereas swamp tupelo rarely sprouts other than in response to mechanical injury. Both are deciduous broad-leaved species. One-year old seedlings were purchased from a local nursery. The red maple seeds were collected from local swamps; the swamp tupelo seeds came from Louisiana. Six hundred seedlings (300 of each species) were lifted in February 1989 and planted within a week. Each seedling was potted while still dormant in a 2.5-l round plastic pot with a peat-cypress mulch soil mix.

The experimental design included three factors: tree species, soil moisture establishment conditions, and method of transpiration inhibition. Three soil moisture conditions were chosen to mimic microsites within natural wetlands: drained soil, soil at field capacity, and flooded soil (referred to hereafter as drained, saturated, and flooded, respectively). Saturated and flooded soil moistures were controlled by placing each potted seedling in a larger, 6-l plastic pot that had a slit in the wall to allow drainage at a set level. The saturated soil treatment was maintained in 5 cm of water in the outer pot; these seedlings had ready access to both water and aerated soil, but the volume of aerated soil was less than in the drained soil treatment. Flooded soil conditions were maintained by keeping the soil surfaces under about 2 cm of water, an adequate depth to

produce anoxic conditions in the highly organic potting soil.

Each seedling was randomly assigned to one of the soil moisture treatments and then placed in 1 of 5 blocks (each block held 18 replicates of each species x soil treatment) under 30% shade cloth. Nutrients were augmented by the addition of time-released fertilizer with micronutrients (3 g / pot). In order to minimize heat absorption by the dark soil, Perlite was spread evenly over the soil surface. Seedlings were maintained under these conditions, with frequent watering, from February 1989 until the transpiration inhibition treatments were applied on 1 July 1989.

Seedlings were measured in late June and again at the end of the experiment in late September. Seedling heights, number of expanded sprouts (axillary buds on the first and second year wood), and lengths of the three longest branches on both the first and second year wood were recorded. An axillary bud was considered to be expanded if it had produced leaves. First year wood was produced as nursery grown seedlings, prior to treatment; second year wood was produced during the current growing season, following experimental treatment. Sprout production was recorded for branches on first and second year wood to aid in detection of patterns of apical dominance. Each stem was marked near each expanded bud with a water-proof marker for consistency with subsequent measurements. Conditions of the seedlings

were noted regularly (e.g., chlorosis, apical stem damage, insect-infestation, death).

The seedling transpiration inhibition treatments were accomplished either by spray application of a commercial anti-transpirant (a terpenic polymer, VAPOR GARD, Miller Chemical and Fertilizer Corp., Hanover, Pennsylvania 17331, USA) to the abaxial leaf surfaces (both species have only abaxial stomata) or by inundation. The anti-transpirant covered the red maple abaxial leaf surfaces very evenly because it was held by the leaf hairs, whereas it tended to bead up on the glabrous swamp tupelo leaves. Many of the treated red maple leaves succumbed to heat stress, presumably as a result of blockage of transpiration, and those trees were removed from subsequent analyses.

Transpiration inhibition treatment by inundation was accomplished by placing potted seedlings established in drained and saturated soils in 6-l plastic pots; flooded soil conditions were maintained with soil surfaces under about 2 cm of water. Seedlings flooded in February and assigned the transpiration inhibition treatment by inundation were given no further treatment. After flooding in both February and July, some swamp tupelo seedlings soon died, which suggested that these individuals were not swamp ecotypes (see Keeley 1979).

Stomatal resistances were monitored regularly for 3 weeks following transpiration inhibition treatments. Three

to 5 replicate measurements in 3 blocks for each treatment combination were made with a steady-state diffusion porometer (LI-COR 1600). Two young, fully expanded leaves were measured on each seedling; incident light level was noted for each reading. The 2 readings per seedling were averaged for analysis. The anti-transpirant stuck to the leaf temperature sensor on the porometer; therefore, only enough measurements were made to ensure that stomatal resistance was increased by this treatment.

Following the anti-transpirant treatments, early morning leaf water potentials were measured on three dates using a pressure chamber. A leaf was cut off the plant at the base of the petiole and placed in a plastic bag with a moistened paper towel until it was measured, all within 5 minutes. Because of time constraints (i.e., measurements had to be completed before the dew evaporated) only 4-5 treatment replicates were measured at each sampling date. No tree had more than one leaf removed for leaf water potential measurements.

Analyses of treatment effects for each species were based on a completely randomized fixed 3-factorial experimental design (block x establishment x transpiration). Growth and sprout production (red maple -  $4 \times 3 \times 2$ ; swamp tupelo -  $3 \times 3 \times 3$ ) used the block-by-treatment interaction as the error term. Flooding was used in two main effects of the model: flooded soil establishment conditions and

transpiration inhibition by inundation. Whereas control-inundated and flooded-inundated seedlings were manipulated identically, they are treated statistically as separate treatment combinations, unless otherwise noted. Repeated measures ANOVAs of stomatal resistance block averages weighted by the number of subsamples in each block were used to describe stomatal response to transpiration inhibition treatments over time. ANOVAs of the leaf water potentials were performed on data combined over the 3 measurement dates. Least square means multiple comparisons further investigated significant effects and interactions of experimental treatments (Freund and Littell 1981). Statistical summaries of results presented in tables are given in the appendix. All analyses were performed using SAS-PC Version 2.

#### Humidity Chamber Experiment

Humidity was controlled in two chambers (120 x 120 x 90 cm wooden frames covered with 4-mil clear polyethylene plastic). The plastic was slashed in a control chamber to allow free air flow into the chamber without altering PAR light levels. A 5.7-l warm steam vaporizer was placed on a rack at the top of the other sealed chamber, the humidity chamber. Ten red maple and 10 swamp tupelo seedlings were randomly selected from trees that had been growing in drained soil since February. Five trees of each species were randomly assigned to the control and humidity chambers.

Seedlings were maintained under elevated humidity for 6 weeks (14 July to 30 August) by running the vaporizer for 9-10 hr each day, starting about 7:30 AM. Temperature, relative humidity and light levels were measured in both chambers, and stomatal resistances were monitored during the first week of humidity treatments. Trees in both chambers were watered frequently.

Stem height, branch length and branch production were measured at the end of September in the same manner as described in the methods for the shadehouse experiment on transpiration inhibition. Effects of treatment on the stomatal resistances of each species were compared using the Wilcoxon Rank Sum Test for 2-location problems (Hollander and Wolfe 1973).

## Results

### Red Maple Field Experiment

Tree description and distribution. Of the 80 trees selected for study in the Withlacoochee State Forest, 55 produced basal sprouts prior to treatment. A total of 169 basal sprouts were counted, with 1-4 sprouts per individual. The average DBH of the red maple trees was 5.03 cm (SD = 1.79,  $n = 80$ ).

Effects of location relative to the swamp edge, relative water depth, and size of parent stem on sprout production prior to treatment were assessed by t-tests for trees

with basal sprouts and trees with no basal sprouts. Occurrence of sprouts was not related to distance from the swamp edge or DBH of the parent stem. The average relative water depth of trees with sprouts was 35.6 cm (SD = 5.1,  $n = 55$ ), which was significantly deeper than for trees with no basal sprouts (mean = 31.5 cm, SD = 6.2,  $n = 25$ ;  $t = 14.85$ ,  $df = 78$ ,  $P < .001$ ).

Sprout production during the growing season following treatment. In October 1989, 5 months following treatment, no red maple trees had died or developed obvious signs of detrimental treatment effects. It was expected that trees with cut canopies would have increased epicormic sprouting immediately below the cut; although there was some epicormic sprouting on a few trees that could be attributed to canopy removal, the response was weak and was not related to basal stem sprout production (see below). Stress due to root removal is difficult to assess, but there was no wilting or other obvious effect of root removal.

Contingency analyses revealed no significant treatment effects on basal sprout production. At the end of the growing season following treatment, there was a total of 74 basal sprouts on 23 individuals. Each of the 8 treatment combinations had 2 to 4 sprouting individuals. Detection of treatment effects using contingency analyses when cell sizes are small is difficult, but examination of the data confirmed that sprouting was very evenly distributed among



treatments. The possible exception was a trend toward higher basal sprout production by trees with cut canopies; 15 trees with cut canopies produced basal sprouts versus only 8 trees with intact canopies. Production of basal sprouts during the growing season was not related to transect location, DBH, or water depth.

Mortality of sprouts produced during the summer was high; 36 died of the 74 basal sprouts produced. The cause of death was apparently complete inundation of sprouts that emerged low on the parent stem and had not had time to grow tall enough to avoid submergence.

Five months after treatment, there were 0-4 individuals with dead sprouts in each treatment and no treatment effect. Again, cell sizes were very small, making the test not conclusive. Trees with cut canopies had roughly twice the basal sprout mortality ( $n = 11$ ) than trees with intact canopies ( $n = 5$ ) but this is likely to be a reflection of their higher rate of sprout production.

Sprout production 1 year after treatment. The slight trend of increased basal sprout production by trees with cut canopies had disappeared by May 1989. Twelve months after treatment, there was an even distribution of 23 individuals producing sprouts among treatments (0 - 3 sprouting individuals per treatment); there were no significant treatment effects.

Despite high basal sprout mortality rates during the previous growing season, there were 90 live sprouts in the spring; roughly 1/3 of these sprouts had survived the winter. Five basal sprouts were found on 3 individuals that had died over the winter. Water levels of local swamps were relatively low during the 1988-89 winter. High basal sprout survival rates through the winter, in contrast with high sprout mortality rates the previous summer, were likely to be due to low water levels during the period of sprout elongation.

#### Intraspecific variation in apical dominance strength.

Although there were no effects of canopy opening, root cutting, or altered light levels on basal sprout production, trees that produced sprouts before the onset of the experiment continued to sprout. Of the 55 trees that had produced basal sprouts by May 1988, 29 produced more sprouts by May 1989; only 6 trees of the 25 trees initially recorded with no sprouts produced basal sprouts. Sprout production by a tree at the end of the year of observation could be predicted by its original sprouting condition ( $G = 5.89$ ,  $df = 1$ ,  $P < .05$ ).

#### Shadehouse Experiment

Effects of soil moisture on seedling condition early in the growing season. Effects of soil moisture establishment conditions on red maple and swamp tupelo seedlings were evaluated by growth patterns and the apparent health of the

seedlings, i.e., their vigor and appearance. Mortality rates of red maple seedlings were very low regardless of the soil moisture condition in which they had been established. High mortality rates of flooded swamp tupelo (Table 4.1) may have been due in part to a mixture of ecotypes among the seeds. Those seedlings with parents from upland habitats would be more likely to be flood intolerant (Keeley 1979).

Seedling physiological state and susceptibility to insect damage were indicated by the occurrence of lateral branches gaining apical dominance over the leader shoot (usually due to damage of the main stem), damage by tent caterpillars (Lasiocampidae), and chlorosis. Whereas initial soil moisture conditions had little effect on the apparent health of swamp tupelo surviving the initial effects of inundation, there were definite effects on red maple seedlings (Table 4.1). Red maple seedlings grown in flooded soil for 4 months, from February to June, were weakened, as indicated by the higher percentage of chlorotic individuals; red maples in drained and saturated soils were significantly less likely to be chlorotic than flooded seedlings (G-test,  $P < .05$ ). Flooded red maples were, however, less prone to infestation by tent caterpillars than seedlings in drained or saturated soils (G-test,  $P < .05$ ); apparently leaf blades on flooded seedlings were too small or tough for the caterpillars to roll into cocoons.

Table 4.1. Physical condition of red maple and swamp tupelo seedlings grown under different soil moisture conditions. Measurements, taken in May prior to transpiration inhibition treatments, are reported as percentages of the sample sizes.

	RED MAPLE			SWAMP TUPELO		
	DRAINED	SATURATED	FLOODED	DRAINED	SATURATED	FLOODED
Mortality:	0	0	3	0	0	18
Secondary leader branch production:	44	74	44	3	3	7
Infestation:*	34	49	18	1	1	0
Chlorosis:	17	3	43	41	32	33
Multistem:	1	4	14	0	1	0
Sample size:	71	72	72	71	71	72

\* Trees infested with caterpillars were removed from the statistical analyses.

Damage to upper leaves and main stem apex of seedlings infested by tent caterpillars resulted from leaf rolling and herbivory; many trees with secondary leader branches (i.e., lateral branches that developed into dominant vertically-oriented branches) were damaged by caterpillars. The percentage of red maple seedlings with secondary leader branches, however, exceeded the number of trees that were attacked by caterpillars. The reason for the weak primary leader shoots of red maple is not known but dead leader branch tips were observed throughout the experiment.

In addition to apical dominance influencing patterns of sprout production, sprout growth is under apical control (Zimmerman and Brown 1980). A multistemmed seedling occurred when at least one older branch had been released and had gained some measure of apical dominance together with the main stem. Soil moisture condition had little effect on the morphology of the swamp tupelo seedlings. Flooded red maple seedlings had more multiple stems than seedlings grown under other soil moisture conditions (G-test,  $P < .05$ ; Table 4.1).

Treatment effects were somewhat confounded because trees infested with tent caterpillars, primarily red maple, had increased sprout production. Other than describing the fate of seedlings established under different soil moisture conditions, measurements of caterpillar infested seedlings were not used in further analyses of treatment effects.

Effects of soil moisture on growth and sprout production early in the growing season. Although effects of soil moisture on seedling conditions differed between red maple and swamp tupelo, the effects on sprout production, stem height, and sprout length were consistent for the two species (Table 4.2). Seedlings of both species growing in flooded soils from February to June had significantly shorter stems and branches than seedlings in either drained or saturated soils; seedling growth did not differ between drained and saturated soils. The general pattern of longer branches on first year wood than on the current year's wood reflects the shorter growing time of the new branches since the onset of the growing season.

Nearly 100% of the seedlings of both species had axillary buds that expanded to some degree regardless of soil moisture condition. Therefore, categorical analysis of sprout production versus no sprout production in response to soil moisture treatment would be of little value; the number of expanded axillary buds, however, was used in further analyses as an index of apical dominance of sprouting. Separating analyses of axillary buds formed during the first year of growth (buds on first year wood) from buds formed during subsequent growth (buds on second year wood) allows discrimination of patterns of apical dominance within individuals.

Table 4.2. Growth and sprout production of red maple and swamp tupelo seedlings grown under different soil moisture conditions. Measurements taken in May, prior to transpiration inhibition treatments, are reported as means (SD). Stem height sample sizes (under SD) are the same for all variables. Caterpillar-infested trees have been removed from calculations. Results of Least Square comparisons for each species are indicated with letters (treatments with different letters are significantly different for  $p < .05$ ). Note: Summaries of ANOVA's on log transformed data are in Appendix A.3.

	RED MAPLE			SWAMP TUPELO		
	DRAINED	SATURATED	FLOODED	DRAINED	SATURATED	FLOODED
<u>Stem height (cm):</u>						
	64.8 A (15.9) 47	64.3 A (17.0) 37	30.5 B (9.5) 57	50.9 A (10.0) 70	50.5 A (9.5) 70	28.7 B (9.8) 59
<u>Total number of expanded axillary buds:</u>						
	13.6 A (9.1)	16.9 A (7.5)	6.5 B (6.3)	19.4 A (7.8)	19.4 A (7.6)	8.2 B (4.6)
<u>Number of expanded axillary buds on the first year wood:</u>						
	6.6 A (6.4)	6.5 A (4.8)	6.3 A (6.4)	12.9 A (5.1)	12.1 A (5.5)	8.1 A (4.6)

Number of expanded axillary buds on the second year wood:

7.0 <sup>A</sup> (5.1)	10.4 <sup>A</sup> (5.7)	0.3 <sup>B</sup> (0.9)	6.5 <sup>A</sup> (5.7)	7.3 <sup>A</sup> (6.5)	0.1 <sup>B</sup> (0.6)
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Average length of 3 longest first and second year branches (cm):

7.3 <sup>A</sup> (7.2)	10.9 <sup>A</sup> (7.7)	2.0 <sup>B</sup> (1.6)	9.8 <sup>A</sup> (3.6)	10.3 <sup>A</sup> (4.8)	1.1 <sup>B</sup> (1.2)
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Average length of 3 longest branches on first year wood (cm):

9.7 <sup>A</sup> (12.0)	13.5 <sup>A</sup> (14.8)	3.8 <sup>A</sup> (3.2)	16.1 <sup>A</sup> (6.4)	15.9 <sup>A</sup> (7.0)	2.1 <sup>B</sup> (2.0)
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Average length of 3 longest branches on second year wood (cm):

4.9 <sup>A</sup> (7.8)	8.4 <sup>A</sup> (8.6)	0.2 <sup>B</sup> (0.8)	3.5 <sup>A</sup> (4.0)	4.7 <sup>A</sup> (5.7)	0.1 <sup>B</sup> (0.9)
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By late June, flooded red maple and swamp tupelo seedling stems had significantly fewer expanded axillary buds than seedlings in either drained or saturated soils (Table 4.2). Whereas expansion of the buds on the first year wood was unaffected by soil moisture condition, there were fewer buds on the second year wood of flooded seedlings. There was essentially no stem growth of flooded seedlings of either species and, consequently, no buds were produced that could expand.

Effects of soil moisture establishment conditions on stomatal resistance. Stomatal resistances of red maple and swamp tupelo seedlings established in drained and saturated soils were not significantly different during the three week measurement period in July. Flooded seedling stomatal resistances progressively decreased with time; stomatal resistances of continuously flooded seedlings during the first week of measurements were significantly greater than the seedlings grown under drained and saturated soil moisture conditions. There were, however, no significant effects of flooding on stomatal resistance among seedlings under any soil moisture conditions during the second and third weeks in which measurements were taken (Table 4.3).

The continued decrease in stomatal resistance of seedlings flooded from February to July did not follow the expected pattern of adjustment to flooding stress with time;

Table 4.3. Mean (SD) stomatal resistances ( $s \cdot cm^{-1}$ ) of red maple and swamp tupelo seedlings in the shadehouse experiment. Sample sizes for week 1 (under SD) are the same for weeks 2 and 3. Least Square comparisons within soil moisture establishment conditions and transpiration inhibition treatments are indicated with letters (treatments with different letters are significantly different,  $P < .05$ ). Note: Summaries of ANOVA's on log transformed data are in Appendix A.4. See text for explanation of analyses with (TOTAL) and without (UNFLOODED) seedlings established in flooded soil.

RED MAPLE					
	DRAIN	SATUR.	FLOOD	TOTAL	UNFLOODED
<u>Week 1:</u>					
CONTROL	0.75 (0.16) 5	0.75 (0.18) 5	2.58 (1.14) 5	1.40 <sup>A</sup> (1.09) 15	0.75 <sup>A</sup> (0.17) 10
INUNDATED	1.66 (0.83) 5	0.94 (0.26) 5	2.48 (1.36) 4	1.64 <sup>A</sup> (1.04) 14	1.30 <sup>B</sup> (0.55) 10
TOTAL	1.21 <sup>A</sup> (0.74) 10	0.84 <sup>A</sup> (0.23) 10	2.53 <sup>B</sup> (1.16) 9		
<u>Week 2:</u>					
CONTROL	0.90 (0.21)	0.90 (0.55)	1.83 (0.88)	1.21 <sup>A</sup> (0.73)	0.90 <sup>A</sup> (0.38)
INUNDATED	1.38 (0.64)	1.55 (1.07)	1.96 (0.98)	1.61 <sup>A</sup> (0.87)	1.47 <sup>A</sup> (0.86)
TOTAL	1.14 <sup>A</sup> (0.51)	1.22 <sup>A</sup> (0.87)	1.89 <sup>A</sup> (0.87)		
<u>Week 3:</u>					
CONTROL	0.73 (0.14)	0.58 (0.10)	1.23 (0.73)	0.85 <sup>A</sup> (0.49)	0.66 <sup>A</sup> (0.12)
INUNDATED	1.13 (0.56)	1.35 (0.71)	0.81 (0.28)	1.12 <sup>A</sup> (0.57)	1.24 <sup>B</sup> (0.64)
TOTAL	0.93 <sup>A</sup> (0.44)	0.97 <sup>A</sup> (0.63)	1.04 <sup>A</sup> (0.59)		

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 SWAMP TUPELO
 

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DRAIN	SATUR.	FLOOD	TOTAL	UNFLOODED
0.98 (0.21) 5	0.72 (0.28) 5	6.18 (6.78) 7	3.05 <sup>A</sup> (4.96) 17	0.85 <sup>A</sup> (0.24) 10
1.10 (0.50) 5	1.46 (0.94) 5	6.16 (6.58) 6	3.10 <sup>A</sup> (4.55) 16	1.28 <sup>A</sup> (0.72) 10
1.04 <sup>A</sup> (0.37) 10	1.09 <sup>A</sup> (0.76) 10	6.17 <sup>B</sup> (6.40) 13		
0.96 (0.33)	1.50 (1.41)	2.28 (1.75)	1.66 <sup>A</sup> (1.42)	1.23 <sup>A</sup> (0.87)
3.01 (0.46)	2.46 (1.58)	2.71 (1.78)	2.73 <sup>B</sup> (1.35)	2.74 <sup>B</sup> (1.02)
1.98 <sup>A</sup> (1.15)	1.98 <sup>A</sup> (1.50)	2.48 <sup>A</sup> (1.70)		
0.75 (0.31)	0.61 (0.26)	1.28 (0.79)	0.85 <sup>A</sup> (0.53)	0.68 <sup>A</sup> (0.29)
4.73 (3.41)	4.54 (3.25)	1.29 (0.25)	3.60 <sup>B</sup> (3.01)	4.64 <sup>B</sup> (3.33)
2.52 <sup>A</sup> (2.97)	2.58 <sup>A</sup> (3.00)	1.28 <sup>A</sup> (0.54)		

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stomatal resistances of seedlings flooded since February should have reached equilibrium by July. It is not likely that the decrease in resistances was due to recovery from inundation, as there were no other indications of recovery (e.g., improved color and increased growth).

Stomatal resistance measurements were taken progressively later in the day during a 3 week period: average light levels decreased and plants were monitored at different points in their diurnal cycles (Table 4.4). Decreasing light levels are not likely to explain decreasing stomatal resistances of flooded seedlings, judging by the lack of a similar response of the other seedlings. The saturation light level of stomates, versus photosynthesis saturation, for these species is less than  $500 \text{ uE} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ , possibly as low as  $200\text{-}300 \text{ uE} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$  (Cowen 1977).

Small increases in water deficit increase stomatal resistance and alter diurnal patterns in stomatal resistance; this response can be attributed to leaf water potential and ABA concentrations (Davies et al. 1981). The pattern of decreasing stomatal resistances of continuously flooded seedlings over the three week measurement period may be due to stress; stomates of the highly stressed, flooded seedlings apparently remain closed longer in the day. Consequently, stomatal resistances measured early in the day would be greater than resistances later in the day. This phenomenon needs further study.

Table 4.4. Mean (SD) environmental conditions during stomatal resistance measurements of red maple and swamp tupelo seedlings in the transpiration inhibition shadehouse experiment.

	Week 1	Week 2	Week 3
Measurement dates	July 4, 5, 7, 8	July 11, 12, 14, 16	July 18, 23
Number of measurements per week	4	4	2
Time of measurements	11:40 AM (0.24 hr)	12:15 PM (1.24 hr)	1:15 PM (2.50 hr)
Temperature (°C)	32.5 (1.7)	34.1 (2.0)	31.9 (1.6)
Relative humidity (%)	52.3 (6.2)	46.9 (4.4)	55.6 (0.6)
PAR (uE·m <sup>-2</sup> ·s <sup>-1</sup> )	993 (187)	805 (146)	508 (162)

Effects of transpiration inhibition treatments on stomatal resistance. Stomatal resistances of seedlings flooded since February were very large in July in comparison with seedlings grown in drained and saturated soils. Anti-transpiration treatment averages that included seedlings flooded since February obscured differences between seedlings in drained and saturated soils. Two analyses of effects of transpiration treatments on stomatal resistance are therefore presented in Table 4.3: the first analyzed treatment effects including all three soil moisture establishment conditions (TOTAL), and the second excluded flooded seedlings (UNFLOODED).

Inundation of seedlings established in drained and saturated soils significantly increased stomatal resistance (Table 4.3). The response of red maple seedlings to inundation, however, differed from the response of swamp tupelo. Stomatal resistances of red maple significantly increased the first week following treatment and remained at the same level for the duration of the 3 week monitoring period (Table 4.3). In contrast, increased stomatal resistances of swamp tupelo were marginally significant during the first week, but continued to increase dramatically over the subsequent 2 weeks (Table 4.3).

Stomatal resistances of red maple seedlings flooded in July did not reach the high levels of resistance recorded for the red maple seedlings flooded since February (Table

4.3). This seasonal effect of flooding is likely to be a consequence of the size and growth vigor of the plant at the time of flooding, especially root system size. Seedlings flooded since February never developed root systems as large as other seedlings, only adventitious roots on the soil surface. Seedlings grown in drained and saturated soils until they were flooded in July were large with well developed root systems, which grew throughout aerated portions of the soil at the time of treatment. Although consistently high stomatal resistances of red maple seedlings flooded in July indicate that they did not recover to control levels, the vigorous initial condition of the trees and rapid development of adventitious roots and hypertrophied lenticels apparently functioned to minimize effects of flooding.

Swamp tupelo seedlings flooded in July developed very high stomatal resistances within 3 weeks of treatment (Table 4.4). Resistances in these seedlings showed no indication of recovering from the effects of flooding by leveling off or by developing a diurnal cycle of reduced resistance late in the day. In fact, stomatal resistances of swamp tupelo flooded in July increased over the 3 week monitoring period with no signs of leveling off. Although these trees were growing vigorously when flooded, few swamp tupelo developed adventitious roots or hypertrophied lenticels (see below). Several of these seedlings did not survive to the end of the growing season.

The effects of the anti-transpirant spray on stomatal resistance of the swamp tupelo seedlings cannot be assessed statistically because of small sample sizes. The tackiness of the anti-transpirant film interfered with porometer use and made measurements difficult. Enough measurements were made, however, to confirm that application of the anti-transpirant increased stomatal resistances to levels of flooded seedlings for at least 3 weeks. Average stomatal resistances of leaves sprayed with the anti-transpirant were  $7.6 \text{ s}\cdot\text{cm}^{-1}$  (SD = 2.3) during the first week after treatment and  $1.8 \text{ s}\cdot\text{cm}^{-1}$  (SD = 0.9) during the third week.

Effects of soil moisture condition and transpiration inhibition on leaf water potential. It was predicted that stomatal resistances would increase in response to inundation and application of the anti-transpirant, but leaf water potentials were not expected to be affected. The effects of transpiration inhibition on plant water relations were different for red maple and swamp tupelo (Table 4.5). Early morning leaf water potentials of red maple were not affected by soil moisture condition or transpiration inhibition. Swamp tupelo seedlings flooded since February, however, had significantly greater leaf water potentials than seedlings grown in either drained or saturated soils. Inundation in July of swamp tupelo seedlings grown in drained and saturated soils generally decreased leaf water potentials but was only significant for saturated seedlings (Table 4.5).



Table 4.5. Early morning mean (SD) leaf water potentials (MPa) and sample sizes for 3 measurement periods (July 10, 14, and 18) of seedlings established in different soil moisture conditions and subjected to transpiration inhibition treatments. Results of Least Square comparisons are indicated with letters (treatments with different letters are significantly different,  $P < .05$ ). Note: Summaries of ANOVA's on log transformed data for each species are in Appendix A.5.

	RED MAPLE				SWAMP TUPELO			
	DRAIN	SATUR.	FLOOD	TOTAL	DRAIN	SATUR.	FLOOD	TOTAL
CONTROL:	-0.08 (0.04) 12	-0.12 (0.13) 12	-0.21 (0.30) 12	-0.14 <sup>A</sup> (0.19) 36	-0.09 <sup>ac</sup> (0.12) 12	-0.07 <sup>c</sup> (0.05) 12	-0.24 <sup>b</sup> (0.23) 5	-0.11 <sup>A</sup> (0.03) 29
INUNDATED:	-0.11 (0.10) 12	-0.10 (0.07) 12	-0.14 (0.09) 12	-0.12 <sup>A</sup> (0.08) 36	-0.16 <sup>ab</sup> (0.21) 11	-0.14 <sup>ab</sup> (0.12) 12	-0.14 <sup>abc</sup> (0.18) 7	-0.15 <sup>A</sup> (0.16) 30
ANTI-TRANS.:	-	-	-	-	-0.08 <sup>ac</sup> (0.06) 12	-0.05 <sup>c</sup> (0.02) 11	-0.18 <sup>b</sup> (0.10) 8	-0.09 <sup>A</sup> (0.08) 31
TOTAL:	-0.10 <sup>A</sup> (0.07) 24	-0.11 <sup>A</sup> (0.10) 24	-0.18 <sup>A</sup> (0.19) 35	-	-0.11 <sup>A</sup> (0.14) 35	-0.09 <sup>A</sup> (0.08) 20	-0.18 <sup>B</sup> (0.16) 24	-

Conditions of seedlings 3 months after transpiration inhibition treatments. The most striking effect of inundation on the seedlings was the difference between species: red maple was able to tolerate inundation stress at least in part through plastic morphological responses, but swamp tupelo showed little plasticity in response to stress and simply languished or died when inundated. The anti-transpirant had no effect on these morphological and physiological characteristics of the seedlings (Table 4.6).

The lack of increased production of secondary leader branches or multiple-stemmed individuals of swamp tupelo in response to flooding or transpiration inhibition suggests that this species does not readily respond morphologically to stress (Table 4.6; but see Keeley 1979 for physiological responses of ecotypes). Hypertrophied lenticels and adventitious roots both indicate physiological and anatomical responses to anoxic-induced stress (see Chapter 1). Swamp tupelo showed neither of these responses (Table 4.6) although the increased stomatal resistance of the flooded seedlings clearly indicated that these seedlings were stressed (Table 4.3).

Red maple seedlings were more plastic both morphologically and anatomically than swamp tupelo seedlings. A high proportion of red maple seedlings in all treatment combinations had secondary leader branches (Table 4.6), more than were recorded the previous June (Table 4.1). The

Table 4.6. Physical conditions of red maple and swamp tupelo seedlings established in different soil moisture levels in September, 3 months after transpiration inhibition treatments. Measurements are reported as percentage of sample size. Mortality sample sizes (under percentages) are the same for all variables.

	RED MAPLE			SWAMP TUPELO		
	DRAINED	SATURATED	FLOODED	DRAINED	SATURATED	FLOODED
<u>Mortality:</u>						
CONTROL	0	9	5	0	15	76
	20	23	44	22	20	49
INUNDATED	0	0	-	74	55	-
	21	21	-	23	20	-
ANTI-TRANSPIRANT	-	-	-	0	5	83
	-	-	-	20	22	24
<u>Secondary leader branch production:</u>						
CONTROL	46	61	43	0	5	6
INUNDATED	65	57	-	9	20	-
ANTI-TRANSPIRANT	-	-	-	15	9	4

Multiple stems:

CONTROL	0	17	18	0	5	2
INUNDATED	10	10	-	9	5	-
ANTI-TRANSPIRANT	-	-	-	0	9	0

Hypertrophied lenticels and adventitious root production:

CONTROL	0	9	30	0	5	2
INUNDATED	57	66	-	0	5	-
ANTI-TRANSPIRANT	-	-	-	0	0	4

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occurrence of secondary leader branches was independent of treatment. It is clear that apical control of red maples was not affected by stress induced by anoxia.

Production of hypertrophied lenticels and adventitious roots by red maple seedlings was related to season of inundation. Fewer red maple seedlings established in flooded soils in February produced these stress alleviating responses than seedlings inundated in July, well into the growing season (Table 4.6). Seedlings established at the beginning of the growing season in flooded soils never produced the root volume of the seedlings established in drained and saturated soils; primary and secondary roots in the latter conditions extended throughout the drained soil volume, but flooded root systems were small and all but the roots on the soil surface appeared atrophied.

As evidenced by poor growth and consistently high stomatal resistances (Table 4.3), flooded red maple and swamp tupelo seedlings remained stressed throughout the growing season. Although growth rates of red maple seedlings flooded for the first time in July were reduced, their stomatal resistances were intermediate between the control seedlings grown in drained and saturated soils and control seedlings flooded since February (Table 4.3). This indicates that at least some anoxia-induced stress in red maple was relieved by production of hypertrophied lenticels and adventitious roots.

Effects of soil moisture and transpiration inhibition on seedling size after 1 growing season. There was little difference in patterns of seedling size and sprout production in June (Table 4.2) from the patterns at the end of the growing season (Table 4.7). Stem extension and production of branches on second year wood, but not on first year wood, of both red maple and swamp tupelo were inhibited by flooding. The inhibiting effects of flooding are very consistent and obvious for seedlings that had been flooded since February; the effects are less apparent for seedlings just inundated in July. The seasonal effect of flooding on growth is likely to be related to seasonal patterns of growth; that is, most of the growth for the year was completed by the time of the transpiration treatments in July.

Inhibition of stem extension was the only significant effect of the chemical anti-transpirant on final swamp tupelo measurements in comparison with control seedlings (Table 4.7). Seedlings treated with the anti-transpirant were consistently smaller than control seedlings both in stem height and branch length, although branch length differences were not significant. This pattern suggests that there is an interaction between stem extension and transpiration rates.

Furthermore, while stem extension and second year branch production were reduced by flooding in both species, size and number of branches on first year wood were not

Table 4.7. Effects of transpiration treatments on stem and sprout size, and sprout number of red maple and swamp tupelo seedlings grown in different soil moistures. Measurements were made in September, 3 months following transpiration inhibition treatments, are reported as means (SD). Stem height sample sizes (under SD) are the same for all variables. Least Square comparisons within soil establishment conditions and transpiration inhibition treatments for each species are indicated with letters (treatments with different letters are significantly different at  $P < .05$ . Note: Summaries of ANOVA's on log transformed data are in Appendix A.6.

	RED MAPLE				SWAMP TUPELO			
	DRAINED	SATURATED	FLOODED	TOTAL	DRAINED	SATURATED	FLOODED	TOTAL
<u>Stem height (cm):</u>								
CONTROL:	97.2 (28.4) 20	109.9 (35.8) 23	50.6 (29.7) 21	85.9 <sup>A</sup> (31.3) 64	100.0 (20.6) 20	98.2 (23.9) 18	34.8 (10.7) 12	83.7 <sup>A</sup> (19.9) 50
INUNDATED:	84.0 (20.7) 22	75.5 (22.9) 23	40.2 (14.9) 23	66.6 <sup>B</sup> (19.5) 68	59.6 (10.3) 17	62.6 (15.7) 18	32.3 (11.8) 10	54.7 <sup>B</sup> (12.8) 45
ANTI-TRANS.:	- - -	- - -	- - -	- - -	83.1 (24.1) 18	75.8 (25.1) 18	31.2 (11.2) 13	66.6 <sup>C</sup> (21.0) 49
TOTAL:	90.2 <sup>A</sup> (25.3) 42	92.3 <sup>A</sup> (34.3) 46	45.0 <sup>B</sup> (23.3) 44		82.0 <sup>A</sup> (25.3) 55	78.9 <sup>A</sup> (26.2) 54	32.8 <sup>B</sup> (11.0) 35	

Total number of expanded axillary buds:

CONTROL:	17.0 (10.3)	16.8 (9.4)	7.8 (10.0)	13.9 <sup>A</sup> (10.6)	20.2 (7.5)	21.6 (6.0)	7.8 (4.5)	17.7 <sup>A</sup> (8.4)
INUNDATED:	13.5 (7.9)	13.6 (7.3)	4.7 (3.4)	10.5 <sup>A</sup> (7.6)	14.3 (7.3)	19.6 (24.7)	6.3 (2.5)	14.6 <sup>A</sup> (16.8)
ANTI-TRANS.:	-	-	-	-	27.0 (5.4)	21.7 (7.6)	7.2 (4.2)	19.8 <sup>A</sup> (10.0)
TOTAL:	15.1 <sup>A</sup> (9.1)	15.2 <sup>A</sup> (8.5)	6.1 <sup>B</sup> (7.1)		20.6 <sup>A</sup> (8.5)	20.9 <sup>A</sup> (15.1)	7.1 <sup>B</sup> (3.9)	

Number of expanded axillary buds on the first year wood:

CONTROL:	4.8 (5.7)	5.0 (4.5)	5.0 (5.2)	4.9 <sup>A</sup> (5.0)	9.7 (4.9)	9.4 (5.5)	6.8 (4.6)	8.9 <sup>A</sup> (5.1)
INUNDATED:	4.5 (4.2)	5.4 (4.0)	4.3 (3.7)	4.8 <sup>A</sup> (3.9)	8.7 (6.1)	13.8 (24.9)	5.7 (2.5)	10.1 <sup>A</sup> (16.3)
ANTI-TRANS.:	-	-	-	-	11.1 (4.6)	8.9 (5.0)	5.4 (4.0)	8.8 <sup>A</sup> (5.1)
TOTAL:	4.6 <sup>A</sup> (4.9)	5.2 <sup>A</sup> (4.2)	4.6 <sup>A</sup> (4.4)		9.8 <sup>A</sup> (5.2)	10.7 <sup>A</sup> (14.9)	5.9 <sup>B</sup> (3.8)	



Table 4.7--continued.

	RED MAPLE				SWAMP TUPELO			
	DRAINED	SATURATED	FLOODED	TOTAL	DRAINED	SATURATED	FLOODED	TOTAL
<u>Number of expanded axillary bud on second year wood:</u>								
CONTROL:	12.2 (8.6)	11.8 (9.7)	2.8 (5.2)	9.0 <sup>A</sup> (9.1)	10.5 (6.9)	12.2 (6.4)	1.1 (2.7)	8.8 <sup>A</sup> (7.4)
INUNDATED:	9.0 (6.7)	8.1 (5.8)	0.3 (0.8)	5.8 <sup>B</sup> (6.4)	5.6 (6.7)	5.8 (5.3)	0.6 (1.9)	4.6 <sup>B</sup> (5.7)
ANTI-TRANS.:	- -	- -	- -	- -	21.0 (7.3)	20.0 (8.9)	1.9 (1.7)	15.4 <sup>A</sup> (10.8)
TOTAL:	10.5 <sup>A</sup> (7.8)	10.0 <sup>A</sup> (8.2)	1.5 <sup>B</sup> (3.8)		10.8 <sup>A</sup> (7.4)	10.2 <sup>A</sup> (7.2)	1.2 <sup>B</sup> (2.5)	

Table 4.7--continued.

	RED MAPLE				SWAMP TUPELO			
	DRAINED	SATURATED	FLOODED	TOTAL	DRAINED	SATURATED	FLOODED	TOTAL
<u>Average length of 3 longest branches on first and second year wood (cm):</u>								
CONTROL:	17.8 (9.7)	23.6 (16.9)	7.9 (8.7)	16.6 <sup>A</sup> (14.0)	23.8 (8.0)	27.4 (8.9)	2.9 (3.3)	20.1 <sup>A</sup> (12.3)
INUNDATED:	15.0 (8.1)	19.9 (11.0)	3.4 (2.0)	12.7 <sup>A</sup> (10.5)	11.6 (3.7)	15.2 (5.8)	1.7 (2.5)	11.0 <sup>B</sup> (6.9)
ANTI-TRANS.:	- -	- -	- -	- -	21.0 (7.3)	20.0 (8.9)	1.9 (1.7)	15.4 <sup>A</sup> (10.8)
TOTAL:	16.4 <sup>A</sup> (8.9)	21.7 <sup>A</sup> (14.2)	5.5 <sup>B</sup> (6.5)		19.1 <sup>A</sup> (8.4)	21.0 <sup>A</sup> (9.3)	2.2 <sup>B</sup> (2.5)	

Table 4.7--continued.

	RED MAPLE				SWAMP TUPELO			
	DRAINED	SATURATED	FLOODED	TOTAL	DRAINED	SATURATED	FLOODED	TOTAL
<u>Average length of 3 longest branches on first year wood (cm):</u>								
CONTROL:	17.0 (20.2)	26.1 (30.5)	9.1 (7.9)	17.7 <sup>A</sup> (22.8)	26.3 (10.2)	29.8 (15.2)	5.6 (6.7)	22.6 <sup>A</sup> (15.0)
INUNDATED:	11.9 (11.7)	19.3 (14.2)	6.2 (4.2)	12.5 <sup>A</sup> (12.0)	17.8 (8.6)	21.3 (7.6)	2.8 (3.1)	15.9 <sup>A</sup> (10.2)
ANTI-TRANS.:	- -	- -	- -	- -	24.0 (8.9)	22.6 (10.1)	3.1 (3.2)	17.9 <sup>A</sup> (12.2)
TOTAL:	14.3 <sup>A</sup> (16.3)	22.7 <sup>A</sup> (23.8)	7.6 <sup>A</sup> (6.3)		23.0 <sup>A</sup> (9.8)	24.6 <sup>A</sup> (11.8)	3.9 <sup>B</sup> (4.7)	

Table 4.7--continued.

	RED MAPLE				SWAMP TUPELO			
	DRAINED	SATURATED	FLOODED	TOTAL	DRAINED	SATURATED	FLOODED	TOTAL
<u>Average length of 3 longest branches on second year wood (cm):</u>								
CONTROL:	18.7 (13.8)	21.1 (19.1)	6.6 (12.4)	15.5 <sup>A</sup> (16.5)	21.2 <sup>a</sup> (12.3)	25.1 <sup>a</sup> (12.2)	0.2 <sup>c</sup> (0.6)	17.6 <sup>A</sup> (14.5)
INUNDATED:	18.2 (15.0)	20.5 (15.2)	0.5 (1.7)	13.0 <sup>A</sup> (15.1)	5.3 <sup>b</sup> (6.6)	9.8 <sup>b</sup> (11.9)	0.7 <sup>c</sup> (2.1)	6.1 <sup>B</sup> (9.1)
ANTI-TRANS.:	- -	- -	- -	- -	18.6 <sup>a</sup> (11.9)	17.4 <sup>a</sup> (11.9)	0.7 <sup>c</sup> (1.9)	13.3 <sup>A</sup> (12.7)
TOTAL:	18.4 <sup>A</sup> (14.3)	20.8 <sup>A</sup> (17.0)	3.7 <sup>B</sup> (9.1)		15.4 <sup>A</sup> (12.6)	17.4 <sup>A</sup> (13.4)	0.5 <sup>B</sup> (1.6)	

affected (Table 4.7). In spite of the fact that swamp tupelo exhibits stronger apical control than red maple and flooding is detrimental to the growth of both species, expansion and extension of axillary buds on first year wood were affected less than growth of new wood when transpiration was inhibited either by flooding in July or with the anti-transpirant.

Effects of soil moisture and transpiration inhibition on growth and sprout production. Effects of soil moisture in which seedlings were established in February were apparent in growth patterns late in the growing season. Both red maple and swamp tupelo seedlings established in flooded soil had reduced main stem and second year branch extension, and expanded fewer second year branches between July and September in comparison with seedlings in drained or saturated soils (Table 4.8). Seedlings of both species grew equally well in drained and saturated soils in spite of less aerated soil volume for seedlings grown in the latter soil.

Inundation in July of vigorously growing seedlings grown in drained and saturated soils had similar detrimental effects on swamp tupelo and red maple seedlings. Stems and second year branches of control seedlings continued to grow but growth of inundated seedlings was significantly reduced (Table 4.8). There is no apparent interaction between season of inundation and growth.

Table 4.8. Effects of soil moisture condition and anti-transpiration treatments on growth and sprout production rates of red maple and swamp tupelo seedlings. Mean differences and standard deviations (in parentheses) between measurements in May and September are given. Results of Least Square comparisons within main effects are indicated for each species with letters (treatment totals with different letters are significantly different at  $P < .05$ . Note: Summaries of ANOVA's on log transformed data are in Appendix A.7.

	RED MAPLE				SWAMP TUPELO			
	DRAINED	SATURATED	FLOODED	TOTAL	DRAINED	SATURATED	FLOODED	TOTAL
<u>Stem height (cm):</u>								
CONTROL:	39.0 (19.8) 18	41.4 (24.0) 21	18.3 (21.3) 21	32.7 <sup>A</sup> (23.9) 60	48.9 <sup>b</sup> (18.0) 20	48.3 <sup>b</sup> (22.5) 18	6.0 <sup>c</sup> (9.8) 12	34.4 <sup>A</sup> (25.7) 50
INUNDATED:	19.4 (17.8) 18	11.8 (20.2) 18	9.5 (12.6) 21	13.4 <sup>B</sup> (17.1) 57	10.1 <sup>c</sup> (5.0) 17	11.3 <sup>c</sup> (10.3) 18	3.3 <sup>c</sup> (7.9) 10	9.1 <sup>B</sup> (8.6) 45
ANTI-TRANS.:	- - -	- - -	- - -	- - -	29.1 <sup>a</sup> (23.2) 18	27.5 <sup>a</sup> (22.5) 18	2.5 <sup>c</sup> (9.2) 13	21.5 <sup>C</sup> (22.9) 49
TOTAL:	29.2 <sup>A</sup> (21.0) 36	27.4 <sup>A</sup> (26.6) 39	13.8 <sup>A</sup> (17.8) 42		30.5 <sup>A</sup> (23.4) 55	29.0 <sup>A</sup> (24.3) 54	3.9 <sup>B</sup> (9.0) 35	

Total number of expanded axillary buds:

CONTROL:	2.4 (10.7)	-0.2 (7.1)	-1.5 (8.2)	1.2 <sup>A</sup> (8.7)	-0.5 (7.6)	0.9 (6.3)	0.5 (2.3)	0.3 <sup>A</sup> (6.1)
INUNDATED:	0.8 (7.6)	-5.3 (8.8)	-2.2 (3.9)	-2.2 <sup>B</sup> (7.3)	-6.0 (5.9)	-0.5 (24.0)	-0.1 (3.1)	-2.1 <sup>B</sup> (15.7)
ANTI-TRANS.:	- -	- -	- -	- -	5.9 (7.2)	3.6 (5.7)	-0.3 (2.8)	3.4 <sup>C</sup> (6.1)
TOTAL:	1.6 <sup>A</sup> (9.2)	-2.6 <sup>A</sup> (8.4)	-0.4 <sup>A</sup> (6.7)		-0.1 <sup>A</sup> (8.3)	1.7 <sup>A</sup> (14.5)	0.0 <sup>A</sup> (2.7)	

Number of expanded axillary buds on the first year wood:

CONTROL:	-2.3 (7.0)	-1.7 (4.3)	-0.9 (5.1)	1.6 <sup>A</sup> (5.4)	-3.9 (4.3)	-4.1 (4.2)	-0.4 (2.8)	3.1 <sup>A</sup> (4.2)
INUNDATED:	-2.1 (5.1)	-3.8 (4.8)	-2.6 (4.2)	-2.8 <sup>A</sup> (4.6)	-3.9 (5.2)	2.2 (24.0)	-0.4 (2.8)	-0.7 <sup>A</sup> (15.5)
ANTI-TRANS.:	- -	- -	- -	- -	-2.8 (4.5)	-1.9 (2.6)	-2.0 (1.5)	-2.3 <sup>A</sup> (3.2)
TOTAL:	-2.2 <sup>A</sup> (6.0)	-2.7 <sup>A</sup> (4.6)	-1.7 <sup>A</sup> (4.7)		-3.5 <sup>A</sup> (5.0)	-1.3 <sup>A</sup> (14.1)	-1.0 <sup>A</sup> (2.5)	

Table 4.8--continued.

	RED MAPLE				SWAMP TUPELO			
	DRAINED	SATURATED	FLOODED	TOTAL	DRAINED	SATURATED	FLOODED	TOTAL
<u>Number of expanded axillary bud on second year wood:</u>								
CONTROL:	4.8 (7.4)	1.5 (7.6)	2.4 (5.4)	2.8 <sup>A</sup> (6.9)	3.4 <sup>bd</sup> (5.0)	5.1 <sup>b</sup> (6.4)	0.9 <sup>de</sup> (2.9)	3.4 <sup>A</sup> (5.3)
INUNDATED:	2.9 (5.0)	-1.6 (6.4)	0.3 (0.8)	0.5 <sup>B</sup> (4.9)	-2.1 <sup>c</sup> (4.0)	-1.6 <sup>c</sup> (3.5)	0.3 <sup>ce</sup> (0.9)	-1.4 <sup>B</sup> (3.4)
ANTI-TRANS.:	- -	- -	- -	- -	8.7 <sup>a</sup> (3.4)	5.5 <sup>b</sup> (5.5)	1.7 <sup>de</sup> (2.7)	5.7 <sup>C</sup> (4.9)
TOTAL:	3.8 <sup>A</sup> (6.3)	.1 <sup>B</sup> (7.2)	1.4 <sup>AB</sup> (4.0)		3.4 <sup>A</sup> (6.0)	3.0 <sup>A</sup> (6.2)	1.0 <sup>B</sup> (2.4)	



Table 4.8--continued.

	RED MAPLE				SWAMP TUPELO			
	DRAINED	SATURATED	FLOODED	TOTAL	DRAINED	SATURATED	FLOODED	TOTAL
<u>Average length of 3 longest branches on first and second year wood (cm):</u>								
CONTROL:	11.9 (7.1)	11.2 (11.4)	5.3 (7.9)	9.3 <sup>A</sup> (9.4)	14.3 <sup>e</sup> (6.7)	18.6 <sup>f</sup> (6.6)	1.8 <sup>cd</sup> (2.7)	12.9 <sup>A</sup> (8.8)
INUNDATED:	5.6 (5.7)	4.2 (9.6)	1.0 (1.5)	3.5 <sup>B</sup> (6.5)	2.1 <sup>cd</sup> (1.6)	4.3 <sup>d</sup> (4.4)	1.0 <sup>cd</sup> (2.6)	2.7 <sup>B</sup> (3.4)
ANTI-TRANS.:	- -	- -	- -	- -	9.6 <sup>a</sup> (6.7)	10.3 <sup>a</sup> (7.5)	0.6 <sup>c</sup> (1.1)	7.4 <sup>C</sup> (7.4)
TOTAL:	8.7 <sup>A</sup> (7.1)	7.9 <sup>A</sup> (11.0)	3.2 <sup>A</sup> (6.0)		9.0 <sup>A</sup> (7.6)	11.0 <sup>B</sup> (8.6)	1.1 <sup>C</sup> (2.2)	

Table 4.8--continued.

	RED MAPLE				SWAMP TUPELO			
	DRAINED	SATURATED	FLOODED	TOTAL	DRAINED	SATURATED	FLOODED	TOTAL
<u>Average length of 3 longest branches on first year wood (cm):</u>								
CONTROL:	7.5 (15.5)	8.2 (17.3)	4.5 (5.3)	6.7 <sup>A</sup> (13.5)	10.5 (17.8)	15.7 (11.5)	3.7 (5.8)	10.7 <sup>A</sup> (9.9)
INUNDATED:	0.6 (13.1)	3.9 (17.8)	1.5 (3.5)	2.0 <sup>A</sup> (12.4)	2.6 (3.1)	3.7 (3.8)	1.4 (3.3)	2.8 <sup>B</sup> (3.5)
ANTI-TRANS.:	-	-	-	-	5.8 (8.9)	6.9 (7.0)	0.4 (3.0)	4.8 <sup>B</sup> (7.4)
TOTAL:	4.1 <sup>A</sup> (14.6)	6.2 <sup>A</sup> (17.4)	3.0 <sup>A</sup> (4.7)		6.5 <sup>A</sup> (7.8)	8.8 <sup>A</sup> (9.4)	1.8 <sup>B</sup> (4.3)	

Table 4.8--continued.

	RED MAPLE				SWAMP TUPELO			
	DRAINED	SATURATED	FLOODED	TOTAL	DRAINED	SATURATED	FLOODED	TOTAL
<u>Average length of 3 longest branches on second year wood (cm):</u>								
CONTROL:	16.2 (10.8)	14.1 (14.2)	6.2 (12.4)	11.6 <sup>A</sup> (13.1)	18.2 <sup>ab</sup> (12.0)	21.6 <sup>b</sup> (8.5)	-0.1 <sup>c</sup> (1.2)	15.0 <sup>A</sup> (12.5)
INUNDATED:	10.6 (11.8)	4.5 (9.0)	0.5 (1.6)	5.0 <sup>B</sup> (9.3)	1.6 <sup>c</sup> (3.2)	4.8 <sup>c</sup> (9.5)	0.6 <sup>c</sup> (2.0)	2.7 <sup>B</sup> (6.5)
ANTI-TRANS.:	- -	- -	- -	- -	14.1 <sup>a</sup> (10.7)	13.6 <sup>a</sup> (11.5)	0.7 <sup>c</sup> (1.9)	10.3 <sup>C</sup> (11.1)
TOTAL:	13.4 <sup>A</sup> (11.5)	9.6 <sup>A</sup> (12.9)	3.4 <sup>B</sup> (9.2)		11.7 <sup>A</sup> (11.8)	13.4 <sup>A</sup> (11.9)	0.4 <sup>B</sup> (1.7)	

The lack of differences in number and length of first year branches between control seedlings and seedlings inundated late in the growing season indicates a seasonal pattern of growth (Table 4.8); axillary buds on first year wood, those buds formed by the end of the prior growing season, expand and extend early in the subsequent growing season. Growth of lateral branches is apparently more related to phenology than environmental conditions.

Application of the chemical anti-transpirant to swamp tupelo leaves resulted in extension rates of stems and branches intermediate between control and inundated seedlings (Table 4.8). In spite of detrimental effects of this treatment on growth, however, swamp tupelo seedlings treated with the anti-transpirant had a significantly greater number of expanded second year axillary buds than control or inundated seedlings (Table 4.8). Although I am unable to corroborate these results for swamp tupelo with effects of the anti-transpirant on red maple, this is evidence that the plant water relations influence apical dominance in swamp tupelo seedlings.

#### Humidity Chamber Experiment

Chamber conditions. Relative humidities in the high humidity chamber ranged from 72% to 84%, 12% to 24% higher than the control chamber (59-60%,  $n = 3$ ; ambient: 52-57%,  $n = 3$ ). The walls of the humidity chamber were continuously covered with water. Temperature in the humidity chamber was

within  $0.5^{\circ}\text{C}$  of the control chamber, which was at ambient temperature ( $32.4^{\circ}\text{C}$  at 3:00 PM). Photosynthetically active radiation (PAR) was reduced roughly 20% by the plastic lining of the chambers (e.g., ambient - 1690 and control -  $1370 \text{ uE}\cdot\text{s}^{-1}\cdot\text{cm}^{-2}$ ).

Effects of increased humidity on stomatal resistance.

The 12-24% increase in relative humidity generally caused a significant reduction of stomatal resistance for both red maple and swamp tupelo. Whereas swamp tupelo stomatal resistances in the humidity chamber were consistently lower than in the control chamber following treatment, stomatal resistances of red maple were less consistent. Red maple stomatal resistances in the humidity chamber only became significantly reduced in comparison with those in the control chamber 6 days following treatment (Table 4.9).

Seedling growth and sprout production in altered humidity. Increased humidity had no significant effect on growth and sprout production of red maple and swamp tupelo seedlings except for increased length of branches on second year wood (Table 4.10). Although few of the measures of stem and branch extension are significant, seedlings of both species in the humidity chamber tended to be larger than their control counterparts. This difference is consistent with the effects of transpiration inhibition measured in the transpiration inhibition shadehouse experiment: as

Table 4.9. Mean (SD) stomatal resistances ( $\text{cm}\cdot\text{s}^{-1}$ ) of red maple and swamp tupelo seedlings in the control and high humidity chambers from 14 July to 30 August. Results of Wilcoxon Rank Sum tests within species (sample size under SD) for each date are indicated with letters (means with different letters are significantly different at  $P < .05$ ).

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	<u>RED MAPLE</u>	<u>SWAMP TUPELO</u>
<u>July 16</u>		
CONTROL CHAMBER	0.94 <sup>A</sup> (0.31) 4	0.80 <sup>A</sup> (0.15) 5
HIGH HUMIDITY CHAMBER	0.67 <sup>B</sup> (0.06) 3	0.36 <sup>A</sup> (0.09) 4
<u>July 20</u>		
CONTROL CHAMBER	0.37 <sup>A</sup> (0.05) 4	0.62 <sup>A</sup> (0.14) 4
HIGH HUMIDITY CHAMBER	0.12 <sup>B</sup> (0.03) 4	0.18 <sup>B</sup> (0.10) 4

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Table 4.10. Measurements of red maple and swamp tupelo seedlings grown from July to October in high humidity and control chambers. Means (SD) are given for size and sprout production measurements made in May, October, and growth (October - May) during the period of increased humidity treatment. Significant effects of humidity on seedling size and sprout production for each species are indicated with letters (treatments with different letters are significantly different at P < .05). Note: Summaries of Wilcoxon 2-sample Tests of humidity effects on growth and sprout production are in Appendix A.8.

	RED MAPLE			SWAMP TUPELO		
	MAY (initial)	OCTOBER (final)	GROWTH (difference)	MAY (initial)	OCTOBER (final)	GROWTH (difference)
<u>Stem height:</u>						
CONTROL	62.3 <sup>A</sup> (22.1) 5	103.8 <sup>A</sup> (15.3) 5	41.5 <sup>A</sup> (21.6) 5	48.0 <sup>A</sup> (8.7) 5	85.6 <sup>A</sup> (10.7) 5	37.6 <sup>A</sup> (13.6) 5
HUMIDITY	50.0 <sup>A</sup> (21.4) 4	102.2 <sup>A</sup> (41.8) 4	52.2 <sup>A</sup> (30.4) 4	51.8 <sup>A</sup> (9.6) 5	92.0 <sup>A</sup> (14.7) 5	40.2 <sup>A</sup> (13.9) 5
<u>Total number of expanded axillary buds:</u>						
CONTROL	23.8 <sup>A</sup> (12.0)	19.5 <sup>A</sup> (8.3)	-4.3 <sup>A</sup> (4.3)	21.0 <sup>A</sup> (8.6)	16.4 <sup>A</sup> (7.6)	-4.6 <sup>A</sup> (4.7)
HUMIDITY	12.8 <sup>A</sup> (8.0)	10.0 <sup>A</sup> (5.5)	-2.8 <sup>A</sup> (3.8)	24.0 <sup>A</sup> (6.2)	18.6 <sup>A</sup> (7.2)	-5.4 <sup>A</sup> (5.9)

Number of expanded axillary buds on first year wood:

CONTROL	13.5 <sup>A</sup> (10.5)	9.0 <sup>A</sup> (7.8)	-4.5 <sup>A</sup> (3.1)	8.2 <sup>A</sup> (2.3)	4.2 <sup>A</sup> (1.3)	-4.0 <sup>A</sup> (2.8)
HUMIDITY	4.0 <sup>A</sup> (2.9)	2.8 <sup>A</sup> (1.1)	-1.2 <sup>A</sup> (2.4)	9.8 <sup>A</sup> (7.6)	5.4 <sup>A</sup> (6.3)	-4.4 <sup>A</sup> (2.5)

Number of expanded axillary buds on second year wood:

CONTROL	10.3 <sup>A</sup> (8.7)	10.5 <sup>A</sup> (8.1)	0.3 <sup>A</sup> (1.3)	12.8 <sup>A</sup> (7.0)	12.2 <sup>A</sup> (7.9)	-0.6 <sup>A</sup> (4.4)
HUMIDITY	8.8 <sup>A</sup> (6.7)	7.2 <sup>A</sup> (5.5)	-1.6 <sup>A</sup> (1.8)	14.2 <sup>A</sup> (4.1)	13.2 <sup>A</sup> (7.2)	-1.0 <sup>A</sup> (5.3)

Average length of 3 longest first and second year branches (cm):

CONTROL	14.5 <sup>A</sup> (9.0)	32.7 <sup>A</sup> (11.6)	18.2 <sup>A</sup> (10.0)	9.9 <sup>A</sup> (2.8)	18.2 <sup>A</sup> (4.6)	8.3 <sup>A</sup> (3.3)
HUMIDITY	7.9 <sup>A</sup> (7.2)	32.1 <sup>A</sup> (20.9)	24.2 <sup>A</sup> (16.0)	12.7 <sup>A</sup> (5.3)	29.9 <sup>A</sup> (9.6)	17.2 <sup>B</sup> (7.0)



Table 4.10--continued.

	RED MAPLE			SWAMP TUPELO		
	MAY (initial)	OCTOBER (final)	GROWTH (difference)	MAY (initial)	OCTOBER (final)	GROWTH (difference)
<u>Average length of 3 longest branches on first year wood (cm):</u>						
CONTROL	20.5 <sup>A</sup> (13.2)	38.3 <sup>A</sup> (26.0)	17.7 <sup>A</sup> (16.4)	16.6 <sup>A</sup> (4.6)	22.8 <sup>A</sup> (4.8)	6.2 <sup>A</sup> (3.4)
HUMIDITY	13.5 <sup>A</sup> (14.6)	34.5 <sup>A</sup> (29.5)	21.0 <sup>A</sup> (19.4)	16.6 <sup>A</sup> (12.1)	25.0 <sup>A</sup> (18.6)	8.4 <sup>A</sup> (7.8)
<u>Average length of 3 longest branches on second year wood (cm):</u>						
CONTROL	8.4 <sup>A</sup> (7.6)	27.1 <sup>A</sup> (7.1)	18.6 <sup>A</sup> (10.3)	3.3 <sup>A</sup> (3.8)	13.6 <sup>A</sup> (9.2)	10.4 <sup>A</sup> (6.4)
HUMIDITY	2.2 <sup>A</sup> (3.6)	29.7 <sup>A</sup> (19.8)	27.4 <sup>B</sup> (17.1)	8.7 <sup>A</sup> (7.8)	34.7 <sup>B</sup> (11.0)	26.0 <sup>B</sup> (9.6)

expected, extension of stems and branches is inversely related to stomatal resistance.

## Discussion

### Mechanisms of Apical Dominance

Explaining the mechanism of apical dominance is a particularly difficult problem in plant physiology and has led to a polarized set of opinions (see Rubinstein and Nagao 1976, McIntyre 1987). Interest in the role of plant water relations in apical dominance has been diverted by the study of hormones, and thus, the theory of bud sink strength relations lacks rigorous testing. In addition, it is not always apparent that the effects of hormones on apical dominance are separate from the effects of plant water relations.

The results of this study do not indicate that either the hormonal theory or the plant water relation theory of apical dominance had ecological significance as mechanisms by which flooding affects basal sprout production by wetland trees. Basal sprout production of red maple trees was not affected by removal of roots or canopies or by changing light and temperature levels on mature red maple tree trunks. This suggests that the effect of flooding on basal sprout production rates is not solely related to altered auxin or cytokinin concentrations resulting from changes in root-to-shoot ratios (Salisbury and Ross 1985). While some epicormic sprout production was noted just below cuts in

some red maple canopies, a common response to damage (Putz and Brokaw 1989), mechanical damage did not cause expansion of axillary buds distant from the cut as would be the case for basal sprouts (but see Ewel 1985).

Whereas flooding red maple and swamp tupelo seedlings inhibited expansion rates of axillary buds on new wood, expansion rates of buds formed prior to treatment (i.e., buds on first year wood of 2 year old seedlings) were not affected. The only treatment, including mechanical damage, humidity, and flooding, that increased sprout production rates was application of the chemical anti-transpirant; swamp tupelo seedlings had the greatest rate of bud expansion on new wood when transpiration rates were inhibited by the anti-transpirant (Table 4.8). This suggests that initial bud expansion, at least in swamp tupelo, is related to a shift in plant water relations.

#### Plant Water Relations of Flooded Seedlings

Inhibiting effects of flooding in February on stomatal resistances of both red maple and swamp tupelo seedlings lasted through July, a very long period of water stress for flood tolerant species (Kozlowski 1984c, Pezeshki and Chambers 1985). The dormant seedlings had apparently been unable to store sufficient carbohydrate and nitrogen reserves prior to flooding in February for metabolic or anatomic adjustments to stress; in comparison with seedlings flooded in July, these seedlings had poor growth rates and

were less likely to develop adventitious roots or hypertrophied lenticels (Tables 4.6 and 4.7). Ability to adjust to anoxia-induced stress is not, however, wholly dependent upon root reserves. Stomatal resistances of seedlings flooded late in the growing season were elevated for at least 3 weeks following inundation, even though most of these seedlings adjusted anatomically to stress (Table 4.6).

Stomatal resistances of flooded seedlings were increased to roughly twice the resistances of seedlings growing in drained or saturated soils, essentially halving transpiration rates (transpiration rate = vapor pressure deficit / resistance). Plant water content of the flooded seedlings remained relatively high. If plant water relations alone control apical dominance, reduction of transpiration rates for 3 weeks should have been adequate to initiate sprouting; sprout production of swamp tupelo seedlings treated with anti-transpirants increased in the same amount of time.

The failure of flooded seedlings to sprout may be due to a number of factors, including insufficient reduction of transpiration rates. Stomatal resistances of flooded seedlings did not reach the high levels produced by the anti-transpirant, and thus transpiration demand for plant water may not have been decreased sufficiently to reduce sink strength of the apical stems; relative sink strength of axillary buds was not increased adequately to access the

plant water still required for transpiration. This is supported by the fact that removal of half the canopies of mature red maples resulted in a reduction of roughly half of the transpiring leaf area but was not adequate to stimulate basal sprout production.

Another possible reason for lack of increased sprouting by flooded seedlings is an overriding toxic effect of flood-induced anoxia. Among the physiological and morphological responses of flooded plants to lack of oxygen for root respiration and accumulation of toxic metabolic products is the aforementioned increase in auxin concentration (Reid and Bradford 1984). Increased auxin concentrations in response to flooding may counteract effects of increased plant water sink strength of axillary buds in sprout production of wetland trees. This suggests that both plant water relations and hormones function together in the control of apical dominance.

#### Transpiration Rates and Humidity

Flooding slowed rates of axillary bud formation by reducing growth rates. However, sprout production by the expansion of preformed buds was not inhibited by flooding (Tables 4.7 and 4.8). Alteration of plant water relations by reduction of transpiration rates has a potential role in increasing sprout production of wetland trees if the characteristically high humidities of wetlands are adequate to reduce transpiration rates (Brown 1981). That is, while the

hydrological cycle in a wetland is not likely to be directly related to the rate of sprout production, the reduced vapor pressure deficit gradient between the leaf and the atmosphere in humid wetlands may reduce transpiration demand for plant water.

Results of the humidity chamber experiment showed that at high humidity levels that are below saturation levels, transpiration rates of both red maple and swamp tupelo were increased due to decreased stomatal resistance. Transpiration rates increase with relative humidity until the vapor pressure deficit gradient between ambient air and leaf atmosphere is essentially zero, at nearly 100% relative humidity, causing transpiration rates to approach zero (Losch and Tenhunen 1981).

Transpiration demand for plant water apparently remains high in wetlands, even during the most humid summer months. For example, diurnal saturation deficit levels in Florida cypress domes during July and September range from 0 - 2 mb, 3 to 9 AM, to a high of 15 - 40 mb, about 3 PM (Brown et al. 1984). Transpiration rates would be low under both of these conditions because evaporation rates would be slow in the morning hours and stomates close under water stress later in the day. During daily periods of intermediate saturation deficit levels, however, transpiration levels would be relatively high (Losch and Tenhunen 1981, Salisbury and Ross

1985). Transpirational demand for plant water, therefore, would vary diurnally in wetlands.

Increased sink strength of lateral buds for plant water in the stimulation of sprouting of wetland trees relies on a reduction of transpiration for a sufficient period of time for the buds to sustain independent growth. Relative sink strength of apical portions of wetland plants for plant water may fluctuate through the day with transpiration rates, but there is little support for the hypothesis that sufficient humidity levels are maintained in wetlands to maintain low transpiration rates.

#### Apical Dominance of Flooded Plants

Flooding has no direct effect on the mechanisms of apical dominance of red maple or swamp tupelo basal sprouts. In spite of altered plant water status and hormonal balance, regardless of the season, basal sprout production rates were not altered by inundation. While both plant water relations and hormones are likely to interact to control basal sprout production, inundation does not affect the physiological status of plants in such a manner as to alter patterns of apical dominance.

Continued basal sprout production by mature red maple trees, in spite of canopy, root, or light treatments, suggests a strong genetic control of apical dominance. Intra-specific variation in strength of apical dominance is likely

to prove to be an important factor in sprout production of populations and a fruitful avenue of research, as well.

#### Sprout Production in Wetlands

The role of flooding in basal sprout production by red maple and swamp tupelo is related to the reduction of axillary bud formation and extension rates, both of which are the result of reduced growth rates. Inundation reduces growth rates of plants primarily through carbon limitation of photosynthesis, caused when stomatal aperture is reduced (Kozlowski 1984a).

Inhibition of growth by flooding leaves sprouts susceptible to submersion by seasonal water level fluctuations. Trees growing in any part of a swamp, in flooded, saturated or drained soils, are capable of producing sprouts. Survival of sprouts in swamps depends on their relative elevation, either by their position on the tree or on a raised microsite, to rising water levels and sufficiently rapid extension growth rates that keep foliage above water.



## CHAPTER 5 SUMMARY AND CONCLUSIONS

### Sprout Production and Growth in Wetlands

Sprout production is common in forested wetlands of north-central Florida. Every forested wetland observed had individuals actively producing both sprouts and large stems of sprout origin. Sprouting stems comprised from 4 to 40% of tree stems in wetlands differing in natural hydrologic conditions and species composition; a similar range was noted for densities of stems of sprout origin.

Proportions of stems of sprout origin in the study wetlands depended on the tree species composition and on growing conditions that enable basal sprouts to avoid inundation. Natural communities with large percentages of dicots were more likely to have larger proportions of stems of sprout origin than communities dominated by conifers. While many conifers such as cypress release prolific sprouts from dormant buds following mechanical damage (Stone and Stone 1954, Brandt and Ewel 1989), less than 2% of cypress stems > 2 cm DBH were established from sprouts under natural conditions.

Dicotyledonous tree species exhibited widely variable patterns of basal sprout production and growth. Many tree

species frequently found in forested wetlands have a large percentage of stems actively producing sprouts as well as a large percentage of stems  $> 2$  cm DBH of sprout origin. For example, red maple and ash had more than 20% of their stems  $> 2$  cm DBH both producing sprouts and established as sprouts. Swamp tupelo represents the low end of the range of sprouting capacity among common dicot species with less than 10% of the stems  $> 2$  cm DBH either producing sprouts or established from sprouts. Species with greatest sprout production capacities also had the greatest probability of sprouts growing large.

#### Effects of Inundation on Vegetative Regeneration

Submersion of leaves during the growing season is often lethal to wetland tree seedlings (Hosner 1960), as well as to sprouts (personal observation). Oxygen becomes limiting for plant respiration when both atmospheric oxygen diffusion rates and photosynthetic production rates are drastically reduced. Respiration rates of leaves are an order of magnitude greater than in other plant organs (Kramer and Kozlowski 1979), making them particularly susceptible to reduced oxygen availability while inundated; there is little effect of inundation on dormant wetland tree seedling survival (Hosner 1960). Regeneration in wetlands is therefore largely dependent on either tolerance or avoidance of leaf inundation.

In order to survive in wetlands, basal sprouts on trees can avoid inundation either by establishment on parent stems above high water levels or extension of leaves above high water levels. Under good growing conditions, sprouts are capable of more rapid growth rates in biomass and height than seedlings, as well as having extended growing seasons by breaking dormancy early (e.g., Auclair 1988). Growth of red maple and swamp tupelo sprouts, however, was inhibited by flooding; a positive correlation between proportions of stems of basal sprout origin and height of hummocks strongly indicates the importance of raised microsites for vegetative regeneration in wetlands.

#### Effects of Inundation on Mechanisms of Apical Dominance

Although stems of sprout origin in natural wetlands were associated with hummocks, production of basal sprouts in natural wetlands was not related to hydrologic regime, neither directly by inundation nor indirectly by environmental characteristics associated with anoxia. Percentages of stems producing sprouts were not related to depth, duration, or frequency of inundation; soil iron concentration was the only environmental parameter correlated with sprout production.

Lack of association between basal sprout production and hydrology of natural wetlands indicates that mechanisms of apical dominance are not related to anoxia-induced

physiological alterations. These results indicate that anoxia-induced changes in hormone balance (Reid and Bradford 1984) and plant water status (Kozlowski 1984a) had no ecologically significant effect on basal sprout production by inundated plants.

Experimental manipulations confirm the lack of relationship between anoxia and mechanisms of apical dominance. Sprout production rates were not significantly different between red maple and swamp tupelo seedlings grown in drained, saturated or flooded soils; season of inundation also had no effect on sprout production.

Potential indirect effects of inundation on basal sprout production included root mortality, and consequently, reduced canopy area and increased light levels on tree boles. However, experimental canopy and root removal and altered light levels on stems of flooded red maple trees had no effect on basal sprout production. In fact, only those individuals producing basal sprouts prior to treatment continued to sprout following these manipulations. There is no convincing evidence that altered root-to-shoot ratios or light levels affect intraspecific variation in basal sprout production capacity of inundated red maple trees.

#### Sprouting and Recovery of Chronically Stressed Trees

Sprouting patterns in Lake Oklawaha indicate there is no water depth threshold for sprout production by flooded

trees; trees produced sprouts throughout each species-specific flood-tolerance range. Increases in proportions of stems of sprout origin with water depth did not result from stimulation to produce sprouts but apparently from increased mortality, presumably death of genetic individuals unable to recover from the initial stress of inundation.

The positive association between proportions of stems of sprout origin and water depth further indicates the importance of sprout production as a regeneration mechanism for individuals recovering from stress. Most, if not all, ash and red maple individuals growing in water depths  $> 0.6$  m were multiple-stemmed as a consequence of sprout growth since inundation in 1968; no regeneration by seedlings of any species was noted in continuously inundated portions of Lake Oklawaha.

#### Intraspecific Variation in Strength of Apical Dominance

Intraspecific variation in apical dominance strength within populations in Lake Oklawaha was apparently reduced with increasing water depth. Individuals with relatively weak apical dominance have been selected for in continuously inundated portions of Lake Oklawaha; it is not clear whether the selection is directly for the ability to sprout or indirectly through a positive association of sprout production with flood-tolerant genotypes. Flood-tolerant individuals that rejuvenate by sprouting, however, will re-

establish in the Oklawaha River floodplain forest if water levels are returned to normal. In this case, importance of vegetative regeneration should remain high in areas that had once been deeply inundated because of the high sprout production capacities of the surviving individuals.

### Vegetative Regeneration in Wetlands

Results from this study indicate that the significant effect of stress induced by flooding on vegetative regeneration of trees in north-central Florida wetlands is sprout survival rates. No evidence was found either experimentally or in natural wetlands to suggest that inundation of root zones affects apical dominance of basal sprouts; sprout production is not directly a stress-induced response to flooding.

Reduced growth rates of flooded trees, however, leaves sprouts susceptible to inundation and subsequent death. Production of basal sprouts and rapid growth of sprouts prior to inundation are, therefore, primary factors in avoidance of inundation, especially if parent stems are situated on raised sites like hummocks. It is for these reasons that vegetative regeneration of wetland trees is most frequently found in wetlands dominated by dicots rooted on raised microsites.

### Consequences of Sprouts in Wetland Populations

Areas in which sprouts are of principal importance in population reproduction, survivorship, and stability are as a regeneration mechanism, a plastic adaptation to changing environments, and consequently, increased longevity of genetic individuals. Populations with high sprout production capacities have advantages in wetlands because vegetative regeneration is less limited by inundation-induced stress than are seedlings. Sprout production rates are less affected by depth of inundation; therefore, sprouting populations have the potential to regenerate and stabilize under a wide range of hydrological conditions, even where seedling regeneration is not possible.

Chances of recovering stress-impacted population densities are increased with long-lived individuals because of their increased likelihood of producing seeds when environmental conditions become conducive to seedling establishment. Although individual swamp gum and cypress have tolerated deep, continuous inundation in Lake Oklawaha for more than 18 years, their regeneration potential ends with their imminent death; ash and red maple apparently will be able to regenerate new stems for a much longer period of time and will be the predominant seed source if water levels are returned to normal.

### Vegetative Regeneration in Mature Seral Stage Communities

Plant community dynamics are dictated by the population dynamics of the component species. Where conditions are more conducive to vegetative than sexual regeneration, populations with large sprout production capacity will be favored and community dynamics will be altered. Stable populations mean low species turnover rates; communities with low species turnover rates are often termed "climax communities".

Seral stages of abandoned fields and sand dunes in temperate North America often succeed through conifer-dominated associations, usually maintained as such by fire, to dominance by dicots (Colinvaux 1986), the group of species most capable of vegetative regeneration. In addition, with release from fire or improved drainage, Laessle (1942) first suggested that the principal stages in wetland plant succession of north-central Florida proceeded through a cypress dominated stage to mixed hardwoods. It is, therefore, no coincidence that vegetative reproduction efforts tend to increase relative to sexual reproduction in late successional communities (Abrahamson 1980).

### Effects of Stress on Reproductive Tactics

Superimposition of environmental disturbances or stress-inducing conditions on regeneration and mortality patterns shifts community dynamics depending on whether the



new conditions are response cues, limitations, or neutral with respect to a trait. Different effects of environmental stress on seedling and sprout establishment and mortality rates affect population and community stem density and composition (Figure 5.1). Species have different ranges of reproductive tactics that are reflected by relative proportions of stems that are of sprout or seedling origin (Keeley 1981). For example, Species A may only be able to reproduce by seeds with no reproductive alternative, whereas co-occurring populations of Species B can range between 100% stems of sprout origin or 100% seedling origin, depending on environmental conditions. Given frequent fires, seed and sprout production may be stimulated for both species, but higher seedling mortality rates in subsequent fires favor stems of sprout origin; Species A would become dominated by Species B. In addition to a lack of stimulus for sprout production, infrequent fires would have fewer detrimental effects on seedling mortality rates; in cases of higher stem proportions of seedling origin, Species A and B would be more likely to occur as codominants. Effects of flood-induced stress are greater on mortality than production rates of wetland plants.

Wetland tree seedling and sprout production are continuous; within a time-frame of several years, periods of exposed soils are likely to coincide with seed production and germination. Hydrologic regimes do not induce seedling

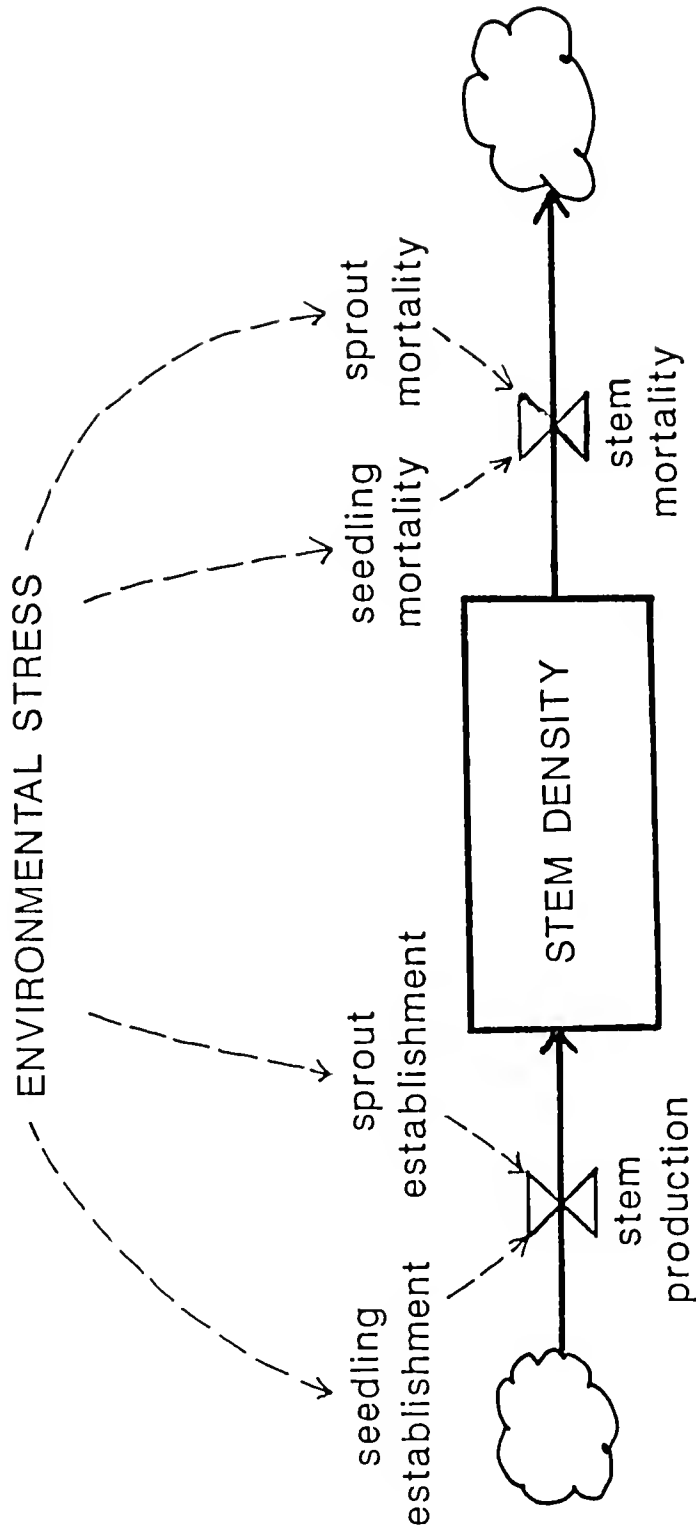


Figure 5.1. Interaction of environmental stress with rates of stem production and mortality of seedlings and sprouts. Environmental stress has differential effects on establishment and mortality of seedlings and sprouts (indicated by 4 dashed vectors from stress to seedlings and sprouts). Production rates of seedlings and stems contribute to population stem production rates, likewise for stem mortality rates (indicated by dashed vectors from seedlings and sprouts to hour-glass rate symbols). Stem density is determined by production minus mortality rates per area (indicated by solid stem input and output lines from stem density state variable). Contributions of seedlings and sprouts to stem densities are the result of differential effects of environmental stress on their respective production and mortality rates.

or sprout production. Stem production rates integrated over several-year periods are therefore unaffected by natural water level fluctuations. Seedling survival, however, is more limited by water level fluctuations than sprout survival when seedlings are unable to avoid submersion. Increased seedling mortality rates increase the success of species capable of sprouting.

Results of these studies suggest that site-specific hydrologic condition leads to population shifts in favor of successful regeneration strategies. Red maple tree sprouting patterns in the Withlacoochee State Forest suggest that sprout production capacity is a genetically controlled trait. Trees in the study swamp were relatively young and first generation occupants of the swamp. Intraspecific variation in sprout production capacity among these individuals remained large, ranging from some individuals never producing basal sprouts to others continually producing sprouts. High sprout production capacities of surviving red maples in Lake Oklawaha, as well as other species, in comparison with natural portions of the Oklawaha River floodplain suggest that intraspecific variation of sprout capacity was reduced by standing water. Patterns of sprout production among natural wetlands further suggest that hydrological interactions may be more limiting to individuals with limited sprout production capacities. Relative importance of vegetative versus sexual regeneration is

therefore a consequence of interactions of the genotype with the response cue/limitation aspects of environmental stress.

#### Vegetative Regeneration in Disturbance-Maintained Communities

Patterns of vegetative regeneration in wetlands are comparable to patterns in disturbance-maintained communities; frequencies and intensities of stress are important in determining relative success of seedlings and sprouts. However, processes by which environmentally induced-stress, such as fire or wind damage, interact with mechanisms of apical dominance and stimulate sprout production are fundamentally different from effects of anoxia.

Sprouting in response to stem loss resulting from forces such as fire or wind serves to restore a balanced root-to-shoot ratio. Regeneration of sprouts in advance of flooding, however, is adaptive in wetlands rather than sprout production in response to flooding. There is no indication that sprouts increase the flood-tolerance of individuals and, therefore, sprout production in response to flooding would have little advantage. Sprouts are only able to regenerate wetland trees when they avoid submersion. In contrast, sprout production in advance of wind, fire, or grazing is wasted effort.

### Maintaining Wetland Processes in a Changing Landscape

With this, then, it is worthwhile to step back and consider wetlands as part of a continually changing landscape, particularly in the presence of people. Changes in the contemporary landscape include fragmentation that limits seed dispersal, altered hydroperiods through draining and drawdown, fire suppression, and logging. Results from Lake Oklawaha show low tolerance thresholds of natural functions to manipulation.

Patterns of relative sprout importance increasing with water depth in Lake Oklawaha differ in fundamental ways from patterns in natural ecosystems. While longevity and vitality of sprouts in the artificially impounded area illustrate the potential for vegetative regeneration of these wetland species, the potential for sexual regeneration is lost. Intelligent use of wetlands depends on understanding their natural processes, including self-perpetuation through sprouting.

### Additional Research of Inundation and Sprouting

Although many questions were raised by these studies, two were of principal importance. In order to understand the ecological role of sprouts in wetlands, it is important to know the genetic relationship between flood-tolerance and sprout production; if there is a correlation between these traits, sprouts may have an additional function in the

physiological recovery of stressed individuals. Furthermore, while patterns of sprout production and establishment were described in these studies, the role of sprouts in wetland population dynamics was only inferred. Long-term studies of stem regeneration and mortality patterns will be necessary to determine the importance of vegetative regeneration in forested wetlands.

## APPENDIX

Table A.1. Summaries of maximum likelihood analyses of hummock height and hydrologic conditions of stems by origin. Data in Table 3.5.

SPECIES	LIKELIHOOD RATIO		INTERCEPT		MICROSITE HEIGHT	
	X <sup>2</sup>	P	coeff.	P	coeff.	P
<u>Acer</u>	119.7	0.32	0.737	0.05	-0.006	0.59
<u>Fraxinus</u>	156.8	<0.01	-0.442	0.12	n/a	
<u>Gordonia</u>	210.3	<0.01	0.702	<0.01	-0.003	0.71
<u>Ilex</u>	218.8	<0.01	0.274	0.21	-0.019	0.08
<u>Magnolia</u>	148.8	0.12	2.942	<0.01	-0.052	<0.01
<u>Nyssa</u>	138.4	0.15	1.444	<0.01	0.054	<0.01
<u>Persea</u>	26.9	0.99	3.504	<0.01	-0.100	<0.01
<u>Taxodium</u>	192.3	1.00	2.448	<0.01	0.039	0.35



DURATION OF INUNDATION		FREQUENCY OF INUNDATION		DEPTH OF INUNDATION	
coeff.	P	coeff.	P	coeff.	P
-0.036	<0.01	0.035	0.03	0.224	<0.01
0.068	<0.01	-0.066	0.03	-0.181	<0.01
-0.051	0.02	0.237	0.06	0.235	0.09
0.009	0.32	-0.120	0.06	0.001	0.97
0.027	0.11	-0.332	<0.01	-0.147	0.04
0.019	0.30	0.143	0.27	-0.023	0.79
-0.076	0.26	-0.202	0.51	0.573	0.22
0.014	0.06	0.026	0.75	-0.006	0.83

Table A.2. Summaries of maximum likelihood analyses of hummock height and hydrologic conditions of stems producing sprouts versus not producing sprouts. Data in Table 3.6.

SPECIES	LIKELIHOOD RATIO		INTERCEPT		MICROSITE HEIGHT	
	$\chi^2$	P	coeff.	P	coeff.	P
<u>Acer</u>	145.2	0.02	-0.232	0.48	0.069	<0.01
<u>Fraxinus</u>	130.4	0.17	1.280	<0.01	n/a	
<u>Gordonia</u>	198.7	<0.01	1.250	<0.01	-0.016	0.07
<u>Ilex</u>	129.8	0.54	1.519	<0.01	-0.022	0.08
<u>Magnolia</u>	168.3	0.01	1.865	<0.01	-0.019	0.15
<u>Nyssa</u>	64.8	1.00	3.141	<0.01	-0.041	0.15
<u>Persea</u>	49.5	0.37	1.963	<0.01	-0.008	0.79
<u>Taxodium</u>	223.7	0.99	2.151	<0.01	0.035	0.30

DURATION OF INUNDATION		FREQUENCY OF INUNDATION		DEPTH OF INUNDATION	
coeff.	P	coeff.	P	coeff.	P
0.017	0.11	-0.012	0.76	-0.028	0.56
-0.033	<0.01	0.010	0.75	0.075	<0.01
0.044	0.10	-0.197	0.16	-0.250	0.12
0.010	0.38	0.032	0.68	-0.073	0.06
-0.005	0.67	-0.158	0.04	-0.042	0.41
0.025	0.25	-0.127	0.44	-0.09	0.27
0.024	0.51	-0.437	0.05	-0.023	0.89
0.031	<0.01	-0.114	0.01	-0.044	<0.01

Table A.3. Analyses of variance summary for growth and sprout production of red maple and swamp tupelo seedlings grown under different soil moisture conditions. Data in Table 4.2.

	ESTABLISHMENT			ERROR	
	df	SS	P	df	SS
RED MAPLE (log transformed data)					
Stem height (cm):	2	19.0	<0.01	6	0.56
Total number of expanded axillary buds:	2	32.21	<0.01	6	3.67
Number of expanded axillary buds on the first year wood:	2	0.45	0.72	6	3.82
Number of expanded axillary buds on the second year wood:	2	120.41	<0.01	6	6.10
Average length of 3 longest first and second year branches (cm):	2	37.12	<0.01	6	3.36
Average length of 3 longest branches on first year wood (cm):	2	9.94	0.17	6	12.37
Average length of 3 longest branches on second year wood (cm):	2	62.73	<0.01	6	13.66

SWAMP TUPELO (log transformed data)

Stem Height:	2	15.17	<0.01	6	1.31
Total number of expanded axillary buds:	2	29.73	<0.01	6	4.12
Number of expanded axillary buds on the first year wood:	2	7.91	0.02	6	2.61
Number of expanded axillary buds on the second year wood:	2	109.38	<0.01	6	7.45
Average length of 3 longest first and second year branches (cm):	2	114.63	<0.01	6	1.75
Average length of 3 longest branches on first year wood (cm):	2	123.04	<0.01	6	2.62
Average length of 3 longest branches on second year wood (cm):	2	52.75	<0.01	6	6.19

Table A.4. Analyses of variance summaries of red maple and swamp tupelo stomatal resistances in the shadehouse experiment. Data in Table 4.3.

	BLOCK			ESTABLISHMENT		
	df	SS	P	df	SS	P
RED MAPLE (TOTAL) :						
WEEK 1	2	0.27	0.44	2	5.57	<0.01
WEEK 2	2	0.12	0.84	2	1.56	0.14
WEEK 3	2	0.44	0.45	2	0.04	0.92
WK 1 VS WK 2	2	0.05	0.88	2	1.34	0.06
WK 1 VS WK 3	2	0.53	0.21	2	4.65	<0.01
RED MAPLE (UNFLOODED) :						
WEEK 1	2	0.01	0.93	1	0.33	0.11
WEEK 2	2	0.07	0.89	1	0.01	0.90
WEEK 3	2	0.37	0.49	1	0.00	0.91
WK 1 VS WK 2	2	0.13	0.71	1	0.25	0.28
WK 1 VS WK 3	2	0.50	0.33	1	0.26	0.28

TRANSPIRATION			E X T			ERROR	
df	SS	P	df	SS	P	df	SS
1	0.60	0.08	2	0.68	0.17	10	1.61
1	0.66	0.19	2	0.20	0.74	10	3.29
1	0.43	0.22	2	1.42	0.11	10	2.55
1	0.00	0.93	2	0.47	0.31	10	1.79
1	0.01	0.75	2	1.14	0.06	10	1.46
1	1.06	0.02	1	0.28	0.14	6	0.10
1	0.89	0.13	1	0.02	0.82	6	1.74
1	1.48	0.05	1	0.18	0.41	6	1.40
1	0.00	0.84	1	0.43	0.17	6	1.08
1	0.04	0.68	1	0.91	0.07	6	1.13

Table A.4--continued.

	BLOCK			ESTABLISHMENT		
	df	SS	P	df	SS	P
SWAMP TUPELO (TOTAL) :						
WEEK 1	2	2.15	0.17	2	13.44	<0.01
WEEK 2	2	3.04	<0.01	2	1.01	0.10
WEEK 3	2	2.50	0.14	2	0.44	0.67
WK 1 VS WK 2	2	0.09	0.85	2	7.26	<0.01
WK 1 VS WK 3	2	4.70	0.04	2	17.3	<0.01
SWAMP TUPELO (UNFLOODED) :						
WEEK 1	2	0.05	0.811	1	0.01	0.76
WEEK 2	2	0.62	0.20	1	0.05	0.57
WEEK 3	2	4.27	0.03	1	0.21	0.43
WK 1 VS WK 2	2	0.55	0.20	1	0.01	0.75
WK 1 VS WK 3	2	3.53	0.07	1	0.13	0.60



TRANSPIRATION			E X T			ERROR	
df	SS	P	df	SS	P	df	SS
1	0.68	0.27	2	0.45	0.65	10	4.98
1	4.26	<0.01	2	1.20	0.07	10	1.68
1	11.95	<0.01	2	6.19	0.02	10	5.30
1	1.54	0.04	2	1.98	0.07	10	2.83
1	6.94	<0.01	2	5.76	0.02	10	5.25
1	0.55	0.07	1	0.42	0.10	6	0.67
1	4.56	<0.01	1	0.27	0.22	6	0.87
1	16.32	<0.01	1	0.00	0.98	6	1.78
1	1.94	<0.01	1	1.36	0.02	6	0.77
1	10.88	<0.01	1	0.44	0.34	6	2.45

Table A.5. Analyses of variance summaries of leaf water potentials of red maple and swamp tupelo seedlings under different soil moisture and transpiration inhibition treatments. Data in Table 4.5.

ESTABLISHMENT		TRANSPIRATION			E X T			ERROR	
df	SS	P	df	SS	P	df	SS	P	df
RED MAPLE (log transformed data):									
Water Potentials	2	2.40	0.14	1	0.03	0.83	2	0.24	0.82
									66
									38.74
SWAMP TUPELO (log transformed data):									
Water Potentials	2	5.68	0.01	2	0.64	0.55	4	5.71	0.04
									81
									43.62

Table A.6. Analyses of variance summaries of effects of transpiration treatments on stem and sprout size, and sprout number of red maple and swamp tupelo seedlings grown in different moisture levels. Data in Table 4.7.

	ESTABLISHMENT			TRANSPIRATION			E X T			ERROR	
	df	SS	P	df	SS	P	df	SS	P	df	SS
RED MAPLE (log transformed data)											
Stem height (cm):	2	14.56	<0.01	1	1.12	<0.01	2	0.28	0.35	15	1.87
Total number of expanded axillary buds:	2	23.43	<0.01	1	0.46	0.34	2	0.07	0.93	15	7.31
Number of expanded axillary buds on the first year wood:	2	0.42	0.76	1	0.57	0.40	2	0.20	0.88	15	11.15
Number of expanded axillary buds on second year wood:	2	69.92	<0.01	1	3.98	0.02	2	1.05	0.42	15	8.60
Average length of 3 longest branches on first and second year wood (cm):	2	40.47	<0.01	1	0.68	0.40	2	1.31	0.50	15	13.43
Average length of 3 longest branches on first year wood (cm):	2	7.49	0.25	1	0.00	0.99	2	1.07	0.81	15	37.65
Average length of 3 longest branches on second year wood (cm):	2	95.8	<0.01	1	2.5	0.21	2	8.21	0.10	15	22.34

SWAMP TUPELO (log transformed data)

Stem height (cm):	2	18.37	<0.01	2	2.14	<0.01	4	0.91	0.5	16	1.22
Total number of expanded axillary buds:	2	23.43	<0.01	2	2.46	0.05	4	1.84	0.30	16	5.49
Number of expanded axillary buds on the first year wood:	2	4.83	<0.01	2	0.19	0.76	4	1.42	0.41	16	5.36
Number of expanded axillary buds on second year wood:	2	64.75	<0.01	2	17.78	<0.01	4	5.44	0.15	16	11.00
Average length of 3 longest branches on first and second year wood (cm):	2	97.36	<0.01	2	4.53	<0.01	4	1.20	0.42	16	4.63
Average length of 3 longest branches on first year wood (cm):	2	82.55	<0.01	2	2.08	0.15	4	0.93	0.75	16	7.78
Average length of 3 longest branches on second year wood (cm):	2	103.86	<0.01	2	22.09	<0.01	4	12.7	0.03	16	14.59

Table A.7. Analyses of variance summaries of effects of soil moisture condition and transpiration inhibition treatments on growth and sprout production rates of red maple and swamp tupelo seedlings. Data in Table 4.8.

	ESTABLISHMENT			TRANSPIRATION			E X T			ERROR	
	df	SS	P	df	SS	P	df	SS	P	df	SS
RED MAPLE (log transformed data)											
Stem height (cm):	2	0.25	0.06	1	0.64	<0.01	2	0.13	0.20	15	0.53
Total number of expanded axillary buds:	2	0.02	0.29	1	0.06	0.02	2	0.02	0.90	15	0.13
Number of expanded axillary buds on the first year wood:	2	0.00	0.61	1	0.01	0.12	2	0.00	0.98	15	0.07
Number of expanded axillary buds on second year wood:	2	0.02	0.05	1	0.02	0.03	2	0.00	0.81	15	0.04
Average length of 3 longest branches on first and second year wood (cm):	2	0.05	0.08	1	0.09	<0.01	2	0.00	0.85	15	0.13
Average length of 3 longest branches on first year wood (cm):	2	0.00	0.92	1	0.08	0.10	2	0.01	0.83	15	0.38
Average length of 3 longest branches on second year wood (cm):	2	0.13	0.01	1	0.10	<0.01	2	0.01	0.79	15	0.15

SWAMP TUPELO (log transformed data)

Stem height (cm):	2	1.04	<0.01	2	0.87	<0.01	4	0.30	0.01	16	0.28
Total number of expanded axillary buds:	2	0.00	0.81	2	0.06	0.04	4	0.05	0.22	16	0.12
Number of expanded axillary buds on the first year wood:	2	0.01	0.40	2	0.01	0.68	4	0.02	0.58	16	0.09
Number of expanded axillary buds on second year wood:	2	0.01	0.03	2	0.09	0.01	4	0.03	<0.01	16	0.02
Average length of 3 longest branches on first and second year wood (cm):	2	0.16	<0.01	2	0.14	<0.01	4	0.05	<0.01	16	0.03
Average length of 3 longest branches on first year wood (cm):	2	0.08	<0.01	2	0.11	<0.01	4	0.02	0.35	16	0.08
Average length of 3 longest branches on second year wood (cm):	2	0.26	<0.01	2	0.12	<0.01	4	0.10	<0.01	16	0.06

Table A.8. Summaries of Wilcoxon on 2-sample tests of measurements of red maple and swamp tupelo seedlings grown from July to October in high and control humidity chambers. Data in Table 4.10.

	INITIAL		FINAL		CHANGE	
	Z	P	Z	P	Z	P
	RED MAPLE					
Stem height:	0.85	0.39	0.37	0.71	0.61	0.54
Total number of expanded axillary buds:	1.35	0.18	1.36	0.17	0.50	0.62
Number of expanded axillary buds on first year wood:	1.35	0.18	0.77	0.44	1.60	0.11
Number of expanded axillary buds on second year wood:	0.12	0.90	0.25	0.81	1.29	0.20
Average length of 3 longest first and second year branches (cm):	0.86	0.39	0.12	0.90	0.86	0.39
Average length of 3 longest branches on first year wood (cm):	0.37	0.71	0.12	0.90	0.12	0.90
Average length of 3 longest branches on second year wood (cm):	1.11	0.27	0.37	0.17	0.35	0.18

	SWAMP TUPELO			
Stem height:	0.73	0.46	0.42	0.68
Total number of expanded axillary buds:	0.21	0.83	0.42	0.68
Number of expanded axillary buds on first year wood:	0.00	1.00	0.32	0.75
Number of expanded axillary buds on second year wood:	0.10	0.92	0.11	0.92
Average length of 3 longest first and second year branches (cm):	0.83	0.40	1.88	0.06
Average length of 3 longest branches on first year wood (cm):	0.00	1.00	0.21	0.83
Average length of 3 longest branches on second year wood (cm):	1.17	0.24	2.20	0.03
			2.09	0.04



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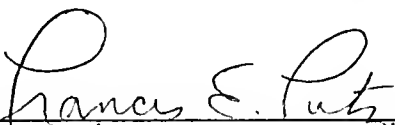
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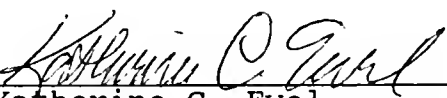
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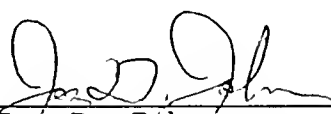
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August 1990

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